The impact of 170 years of flow regulation on processes and patterns in an eastern Tasmanian river system

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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Sandy Bay, Tasmania

October 2011

"*No river can be more dangerous and uncertain than the Macquarie – in winter an impetuous torrent; in summer a mere chain of occasional stagnant ponds; and yet, in all probability, this stream …should impart life and vigour to one of the finest districts in the island, and will be made available for so desirable a purpose*" (D. Burn, 1840)

Permanent pool on the Macquarie River,
with Tooms River entering on the right, above the gravel bar.

"*I have not turned back water at its springtide.*

I have not broken the channel of running water."

The Egyptian book of the dead (Budge 1967)

Declaration of Originality

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Statement of Co-Authorship

Publications produced as part of this thesis:

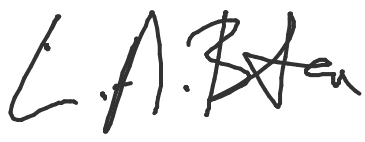
Chapter 6.1: Watson, A. and Barmuta, L.A. (in review) Stable isotope analyses demonstrate that long-term river regulation results in unexpected shifts in food webs, *Freshwater Biology.*

Chapter 6.2: Watson, A. and Barmuta, L.A. (2011) Feeding preference trials confirm unexpected stable isotope results: freshwater macroinvertebrates do consume macrophytes, *Marine and Freshwater Research* **62**: 1248-1257.

The following individual and institutions contributed to the publication of research undertaken as part of this thesis:

Associate Professor Leon. A. Barmuta (University of Tasmania and Tasmanian Aquaculture and Fisheries Institute) assisted with guidance and supervision of all aspects of the Ph.D. and in producing publishable manuscripts.

The undersigned agrees with the above stated proportion of work undertaken for each of the above submitted peer-reviewed manuscripts contributing to this thesis:



Associate Professor Leon. A. Barmuta

(Candidate's supervisor)

Abstract

The flow regime of Tooms River, a tributary of the unregulated Macquarie River in eastern Tasmania, was modified in 1840 by a shallow dam in its upper reaches, resulting in reversed seasonality of high and low flows: a classic, long-term example of a river subjected to "anti-drought", but without the confounding thermal effects of impoundment stratification. I found surprisingly large differences between sites on this regulated branch and sites on the adjacent unregulated branch of the Macquarie, which persisted for 8 km downstream despite tributary inflows. This 2-year comparative study coincided with a prolonged supra-seasonal drought, which enabled examination of the effects of reduced stream flow on both regulated and unregulated examples of confined rivers in a naturally variable climatic regime. The regulated sites remained distinct from the unregulated sites, in terms of riparian litter fall, biofilm abundance and macro-invertebrate diversity.

This is one of very few studies of the long-term effects of flow regulation (e.g. see Kondolf and Batalla 2005; Sheldon and Thoms 2006b), and differs from the majority of regulated river studies in that the effects of regulation of Tooms River are not confounded by land use practises or thermal stratification of the reservoir. However, this impoundment is typical of small irrigation impoundments in Mediterranean and semi-arid climate zones. The ecological consequences of drought and "anti-drought" in a region with a naturally variable flow regime may inform management of biodiversity in other regulated rivers in similar climate zones. Human population increases and climate change pressure on water supplies are likely to increase the demand for many more dams of this size and type of flow alteration (Benstead *et al.* 1999). The determination of the long-term effects of flow regulation is essential, so that future decisions on water allocations can be based on better knowledge of the impact on downstream ecosystem services.

Abstract

Prolonged regulation of the flow regime of Tooms River has had major effects. Regulation has not only reversed the seasonality of flow, but has also dramatically reduced flow variability, resulting in contraction of the stream channel immediately downstream of the dam, and the establishment of mature eucalypts close to the channel, in contrast to the shrubby riparian vegetation maintained by the variable flow regime of the Macquarie River. The timing of allochthonous litter inputs to the benthos was altered, with peak litterfall delayed until irrigation demand fell at the end of summer. In addition, there was reduced lateral connectivity, with movement of leaf litter between the riparian zone and the benthos dependent on overland flow. As predicted by other studies, biofilms were more abundant in the regulated river, but the closed canopy immediately downstream of the dam did not suppress autochthonous productivity, against expectations. Chlorophyll *a* analyses indicated an autotrophic system, dominated by cyanobacteria and diatoms, in contrast to filamentous algae and diatoms in the unregulated river.

Macroinvertebrate communities were significantly different between rivers, but also between sites within rivers, with a depauperate fauna closest to the dam. There was partial recovery of regulation effects at the downstream regulated site, but the invertebrate fauna remained distinct to the unregulated river. In contrast to the majority of studies, there was little difference in invertebrate species richness or evenness between sites or rivers, but diversity was marginally higher at the unregulated sites. Invertebrates from the adjacent Macquarie River were expected to colonise lentic habitats in the regulated river during the drought, but this did not eventuate, suggesting that there may be significant barriers to dispersal or colonisation.

Stable isotope analyses indicated a clear separation of the invertebrate food webs of the two rivers. Although both rivers had abundant leaf litter, terrestrial resources were a minor dietary component in both

rivers. Vascular macrophytes dominated unregulated river diets, while cyanobacteria were more important in the regulated river. Feeding preference trials for the dominant terrestrial leaf species and for macrophytes showed few preferences for terrestrial leaves, despite large differences in toughness, C: N ratios and tannin content. Unlike other Australian and overseas studies, most invertebrates showed a clear preference for the macrophyte *Triglochin procerum*. This was supported by the stable isotope analyses and suggests that the prevalence of macrophytes in invertebrate diets may be underestimated in many food web studies.

It is likely that similar long-term effects will eventuate in other regulated rivers in Mediterranean climate zones as irrigation dams mature.

Acknowledgements

This thesis began as a simple project, and evolved into a monster which has dominated my life and that of my family and friends for far too long. Firstly, special thanks to my partner, Kerry, for his constant love and enthusiasm, for many days of field assistance, and for financial support when my scholarship ran out. Secondly, thanks to my supervisor and mentor, Assoc. Professor Leon Barmuta, who was always encouraging, even when I ignored his excellent advice to avoid working with macroinvertebrates. He showed amazing dexterity with R, and could always find something interesting to examine at a field site, however bad the weather. Dr Alastair Richardson gave feedback on several chapter drafts, while Dr Jenny Davis gave invaluable advice while Leon was on leave in 2007.

Very special thanks to the staff of the Tasmanian Department of Primary Industries, Parks, Water and Environment. Danielle Warfe sourced the major project funding via the TEFlows project, which was supported by NRM North and NRM South under the National Action Plan for Salinity and Water Quality (Project number NAP08). Adam Uytendaal provided support and advice after Danielle moved to a wetter and warmer climate, and also attracted the leeches away from myself and Mike Male over the 4 long days it took to survey the river channels. Scott Hardie took over when Adam moved to an island without leeches. Shivaraj Gurung modelled the hydrology for the ungauged Macquarie River sites. Kathryn Jerie suggested the Tooms River - Macquarie River comparison, which gave this project a strong focus when the drought intervened in the original flood study, while Lois Koehnken helped interpret the mysteries of geomorphology.

The University of Tasmania and School of Zoology supported me with a postgraduate research scholarship for 3½ years, and the Holsworth Wildlife Research Fund provided additional project funding for the

expensive stable isotope and nutrient analyses. Hickman Holloway Constructions donated the Astroturf for the litter fall study and the Watson family (unrelated) kindly allowed me unrestricted access to Tooms River across their property, Blanket Bottom. The School of Zoology and Australian Society for Limnology subsidised my 2007 presentation to the Limnology Conference in Queenstown, New Zealand. Professor B.F.J. Manly made his software available for computing the selectivity index for the feeding preference trial and Hugh Fitzgerald, of the School of Plant Science, conducted the tannin assays.

The field component of this project would have been impossible without assistance from family, friends and student volunteers. Thank you to Ashley Edwards for organising the student volunteer programme, and (in alphabetic order) to Jarrod Adcock, Kaylene Allan, Phil Bonney, Simon Brain, Ryan Burrows, David Carpenter, Lisa Cawthen, Simon Curtis, Danait Ghebrezgabhier, Tom Jackson, Emma Kingston, Mike Male, Raphaela Matuszek, Raylea Parr, Sarah Pyke, Hayley Ricardo, Jacqui Shelton, Christiane Smethurst, Adam Uytendaal and Karen, Kerry, Michelle, and Tim Watson, who all helped with field work, sometimes in trying conditions and always with 4½ long hours of travel time. Michelle also corrected many ambiguities in this thesis and gave invaluable editorial advice on chapter and paper drafts.

Thanks also to fellow postgrads, honours students and researchers, for making the long days at the microscope or computer go faster, especially to Tom & Ivana Karanovic, Louise Newman, Ryan Burrows, John Gooderham and Joanne Clapcott. The Zoology technical and office staff were always cheerful and happy to provide logistic support and distractions in the tea room. Special thanks to Kate Hamilton, Barry Rumbold, Wayne Kelly, Adam Stephens, Simon Talbot, Richard Holmes, Sherrin Bowden and Felicity Wilkinson.

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Chapter 1 General introduction

Climate change is predicted to increase the frequency and severity of both droughts and floods in eastern Australia (Grose *et al.* 2010). While higher rainfall is predicted for eastern Tasmania, the increase in air temperature due to the more southerly migration of the East Australia Current is likely to increase evaporation rates, leading to a decrease in annual runoff into rivers and increased flash flooding with greater soil hydrophobicity. At the same time, community pressure has increased to build more dams, chiefly for agricultural irrigation. As elsewhere, climate change is being used as a further justification for more, often smaller impoundments to either mitigate or take advantage of opportunities presented by climate change (e.g. http://www.tidb.com.au/). However Graf (1999), among others, suggests that climate change is likely to have less impact on riverine ecosystems than has already occurred as a result of flow regulation, which prompted this investigation of the impacts of a smaller impoundment on a Tasmanian river, which has regulated flow for irrigation for over 170 years. The size of this impoundment and type of flow alteration is likely to typify dozens of other proposals in similar climate zones around the world (cf. Benstead *et al.* 1999).

1.1 Ecological background

Climate and geology are the major drivers of the physical components of riverine ecosystems (Poff and Hart 2002), with the interaction between these factors controlling water movement, soil formation and riparian vegetation growth (Petts 1984). Within this context, the flow regime is the fundamental force controlling the river channel, substrate and sediment transport (Graf 1988), which in turn influence riparian communities (Junk *et al.* 1989) and aquatic biota (Ward 1992). Although there is unidirectional longitudinal flow within a river, there is also lateral connectivity with the riparian zone and greater catchment

area, as well as vertical connectivity with the hyporheos, groundwater and atmosphere, with the strength of these connections varying along a river's length (Ward and Stanford 1983b; Ward 1989; Stanford and Ward 1993; Walker *et al.* 1995; Ward and Stanford 1995a) (Fig. 1.1). Loss of this connectivity influences organic material pathways, nutrient flows, and aquatic animal food resources and migration (Bunn and Arthington 2002).

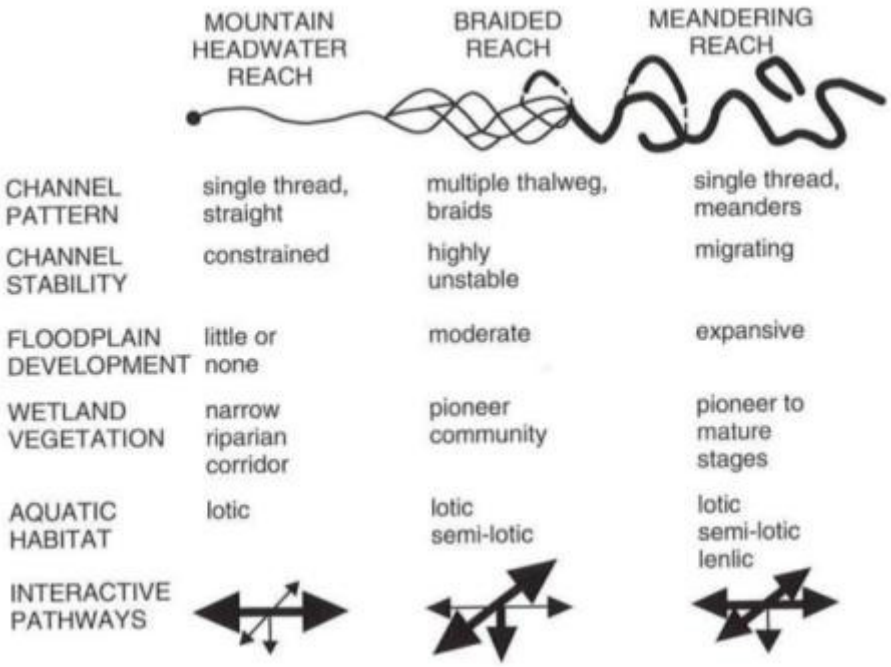


Fig. 1.1 Characteristics of river channels and riparian zones for 3 contrasting river reaches (Ward and Stanford 1995b). The strength of connections between longitudinal (horizontal arrows), vertical and riparian (oblique arrows) zones in each reach type are indicated by the size of the arrows.

The riparian zone is the interface between the stream channel and the surrounding landscape (Gregory *et al.* 1991), an ecotone with characteristics of both environments (Nilsson and Svedmark 2002). Here, "riparian vegetation" refers to the plant community which is susceptible to changes in the water table or overbank flows (Naiman and Décamps 1997) in response to fluvial and geomorphic processes (Merritt *et al.* 2010). It includes vegetation which either shades at least part of the stream or contributes organic material to it (Gregory *et al.*

1991). The flow regime strongly influences the establishment and growth of riparian vegetation (Hupp and Osterkamp 1996; Nilsson and Svedmark 2002), by controlling soil moisture gradients and biochemistry, which impact on physical attributes and species composition of the plant community (Merritt *et al.* 2010).

The riparian zone can have a major influence on the balance between allochthonous and autochthonous resources in the stream, and hence the biota dependent on those resources (Fisher and Likens 1973; Cummins 1979; Vannote *et al.* 1980; Cummins *et al.* 1984; Junk *et al.* 1989). This transfer of nutrients and biota between the riparian zone and the stream is recognised as an important energy pathway (Vannote *et al.* 1980; Junk *et al.* 1989; Thorp and Delong 1994). In confined rivers with forested catchments, control of light and shade by the riparian canopy affects in-stream productivity (Bunn *et al.* 1999) and the production and movement of nutrients (Pusey and Arthington 2003), and may be the major influence on aquatic communities (Bis *et al.* 2000).

Variation in the natural flow regime influences the availability of in-stream and riparian habitats, food resources and nutrient flows, and has a strong influence on biodiversity (Poff *et al.* 1997; Richter *et al.* 1997; Puckridge *et al.* 1998; Hart and Finelli 1999). In this way, flow variability drives ecological variation (Puckridge *et al.* 1998; Bunn and Arthington 2002; Junk and Wantzen 2004), with small pulses in flow important at different habitat scales (Puckridge *et al.* 1998). Life history strategies of aquatic species may have evolved in response to this variation, with seasonal or predictable flow and temperature cueing reproduction in many species, as well as metamorphosis and emergence in many insects (Bunn and Arthington 2002; Humphries and Baldwin 2003). However, as Ward and Stanford (1995b) pointed out (Fig.1.1), all these factors are influenced by the position of the study reach in the stream hierarchy.

1.2 General effects of river regulation

River regulation is defined in this study as the "anthropogenic control of flow in lotic habitats" (Stanford and Ward 1979). McMahon and Finlayson (2003) described regulation for irrigation supply in seasonal climates as "anti-droughts", because the natural, seasonal low flows and cease-to-flow events are replaced by persistent low flows. They contend that this will have far greater impacts on ecosystem health, diversity and community structure than droughts or floods, while Naiman *et al.* (1995) nominated flow regulation as the greatest challenge to riverine ecological sustainability.

The majority of rivers worldwide has been regulated in some form (WCD 2000; Nilsson *et al.* 2005), with some dams thousands of years old (Baxter 1977). However, the worldwide boom in dam building began in the 1930s, with demand for irrigation, water supply and increasingly, hydro electricity production (Graf 1999). Graf (1999) estimated that there were at least 75 000 dams in the US alone, with many more likely to have been built since that date. Over 60% of the rivers in the northern third of the world have some form of flow regulation (Dynesius and Nilsson 1994). Vörösmarty *et al.* (1997) have calculated that 61% of the worlds' fresh water runoff is captured by large dams over 15 m high. However, this does not include approximately 800 000 small dams (WCD 2000) or the millions of farm dams (Naiman *et al.* 2005), which are likely to have a significant impact on river runoff. An irrigation dam built on the Wimmera River in Victoria in the 1850s was the first engineered dam in mainland Australia (Ingle-Smith 1998), but since then at least 446 large dams over 10 m high (Kingsford 2000) and many thousands of smaller weirs have been built. This includes over 3600 locks and weirs in the Murray-Darling River system alone (Arthington and Pusey 2003).

Many studies have examined the effects of dams on downstream ecosystems (e.g. Nilsson *et al.* 1991; Kondolf 1997), but these have largely focussed on large dams, many of which were built in the late 20th century. Similarly, Benke (1990) only considered rivers longer than 200 km in his paper, which lamented the loss of free-flowing rivers in the USA. This focus is typical of regulation studies, which seem to consider that only large dams on major rivers can have a strong impact (Bergkamp *et al.* 2000; Nilsson *et al.* 2005). This is partly because the effects of larger impoundments are more immediate and tend to be closer to populated areas (Stromberg *et al.* 2007). However, the effects of dams are often confounded by the increased agricultural, industrial or urban development that can follow dam construction (Baxter 1977) and this can make it difficult to untangle the effects of regulation effects per se from the other changes in catchment land use. For example, agriculture expanded onto the previous floodplain of an impounded Californian river, displacing the natural riparian vegetation and confounding regulation effects (Gordon and Meentemeyer 2006).

The international peer-reviewed literature is heavily focussed on hydro-electric and multiple impoundments (e.g. Angradi 1994; Pomeroy *et al.* 2000; Vinson 2001). Within Australia, the focus has been on the large floodplain rivers of the southeast, such as the Murray-Darling River system (e.g. Sheldon and Walker 1997; Baldwin *et al.* 2009), most of which were regulated in the late 19th- to mid- 20th century (Walker 1985). Graf (1999) suggested that many dams have not been in place long enough for full downstream effects to emerge. There is now a focus in the USA and Europe to remove some of the older, and typically smallest, dams. For example, Hart *et al.* (2002) reviewed downstream effects of the removal of 20 dams, ranging from 2 – 17 m high and in age from 27 – 162 years. Although Poff and Hart (2002) suggested that small dams may have limited ecosystem effects, Benstead *et al.* (1999) showed that even a 1.2 m high dam could affect anadromous biota.

Benstead *et al.* (1999) further emphasised the lack of ecological studies on small dams and noted that future irrigation projects in developing countries are likely to involve small dams in more marginal climate zones.

Dam construction has an immediate effect on river flow, initially increasing sedimentation of the channel (Williams and Wolman 1984), but ultimately reducing energy and material transfer from the upper to lower reaches of the river. Subsequent changes to the channel form and productivity gradient are a slow process which may not reach equilibrium for up to a century (Petts 1984). The loss of sediment behind the dam increases the kinetic energy and erosional power of the water below the dam. These effects can be transmitted a considerable distance downstream, and may dramatically reduce sedimentation rates on floodplains or at the river delta (Petts 1984). Conversely, reduced stream power can also increase sedimentation in the river, which can smother interstitial spaces and hyporheic habitats (Kondolf 1997). Where the channel is incised, the river can contain a greater discharge before overbank flows occur, reducing floodplain inundation frequency (Bergkamp *et al.* 2000). The degree of channel adjustment is a function of the post-dam discharge, sediment supply and substrate size (Grant *et al.* 2003). This has been estimated by Petts (1980) to extend downstream until the impoundment comprises less than 40% of the overall catchment. However, Gregory and Park (1974) showed that channel contraction on the River Tone in the UK extended until the total catchment was more than 4 times the size of the impoundment. According to Walker (1985), any recovery from impoundment is likely to be confounded by other anthropogenic effects.

While some impacts are common to all impoundments, other factors depend on the size of the reservoir and the overall purpose of regulation (Camargo and Voelz 1998) and whether the impoundment is in the headwaters or lowlands (Brittain and L'Abée-Lund 1995; Grant *et al.*

2003). In contrast to flood control and hydro-electric supply dams, irrigation dams decrease flows in winter when the reservoir is filling and increase flows in the normal dry season (e.g. Fig. 1.2), when irrigation demand is highest (e.g. Petts 1984; Reich *et al.* 2009). In this case, floods can only occur through dam spillage when the storage is at maximum capacity, while natural, seasonal low flows are suppressed by water releases in summer (Petts 1984; Kondolf and Batalla 2005).

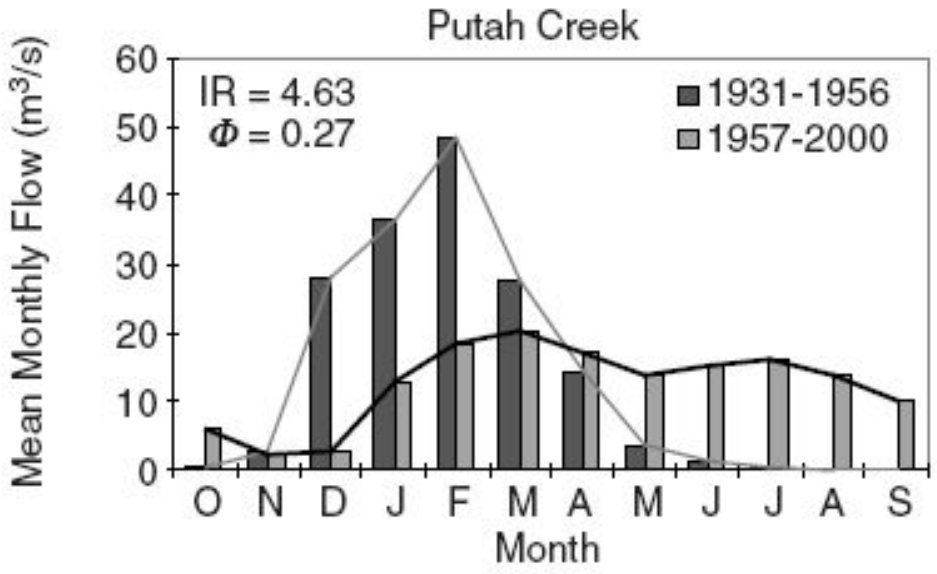


Fig. 1.2 Mean monthly flow ($m^3.sec^{-1}$) for Putah Creek, a tributary of the Sacramento River in California, contrasting pre-impoundment discharge with flow after the 1956 construction of Monticello Dam. IR is the Impounded Runoff Index, where an IR of 1.0 indicates that water is retained for 1 year in the reservoir. Φ is the pre-dam, post-dam correlation coefficient. A value of 1.0 indicates close correlation between the pre-dam and post-dam monthly flow regimes. Winter peak flows were eliminated by the dam, while summer low flows were augmented by irrigation releases (Kondolf and Batalla 2005).

More importantly, irrigation impoundments ultimately reduce downstream discharge, because, unlike hydro-electric supply dams, abstracted water is not directly returned to the river (Kondolf *et al.* 1996; Bergkamp *et al.* 2000; Nilsson *et al.* 2005). In semi-arid areas, drainage from irrigation can also increase salinity in downstream reaches (Bergkamp *et al.* 2000).

The high surface area to volume ratio of the reservoir results in warmer temperatures, and subsequent thermal stratification of deep, sheltered water bodies (Petts 1984; WCD 2000). In addition, the different densities of water entering and stored in the reservoir can produce density currents and chemical stratification (Petts 1984). The water temperature below the dam depends on whether warm surface water or cold bottom water, typical of hydro-electric storages, is released (Vinson 2001; Poff and Hart 2002).

Irrigation impoundments in Mediterranean climates typically feature a reversed flow regime, loss of summer low flows and reduced flood frequency. This impacts on the abundance and community structure of the riparian vegetation (Merritt and Cooper 2000; Nilsson and Berggren 2000; Stromberg *et al.* 2007), algal communities (Ryder *et al.* 2006) and aquatic macroinvertebrates (Boulton and Lloyd 1992), which in turn affect nutrient cycling (Ahearn *et al.* 2005) and riparian seedling recruitment (Rood and Mahoney 1990; Auble and Scott 1998). Moreover, the lack of disturbance may be reflected in reduced resistance and resilience of invertebrate communities to stochastic events in regulated systems (e.g. references in Reice *et al.* 1990).

The effects of river regulation have been well documented (Table 1.1), with an excellent early review by Petts (1984) and more recent reviews by Bergkamp *et al.* (2000); Bunn and Arthington (2002); Lloyd *et al.* (2003); Poff and Zimmerman (2010); WCD (2000), among others.

Table 1.1 Examples of published studies of river regulation. Many impoundments impact on several ecosystem processes, with the earliest studies of dams built in the late 1800s.

Ecosystem process	Impoundment date	Impact	Reference
Modified flow regime	1. 1923-1979; late 1800s	1. Reduced discharge, smaller floods	1. Kondolf and Batalla (2005); Nichols *et al.* (2006)
	2. 1923-1979	2. Less frequent floods	2. Kondolf and Batalla (2005)
Changes to river channel	1. 1988; 1900s; 1983	1. Channel incision	1. Choi *et al.* (2005); Collier *et al.* (1996); Gordon and Meentemeyer (2006)
	2. 1962; 1915-1968	2. Channel contraction	2. Merritt and Cooper (2000); Nichols *et al.* (2006)
	3.1960s; 1915-1968	3. Bed armouring	3. Kondolf (1997); Nichols *et al.* (2006)
	4.1880s-1950s	4. Reduced channel complexity	4. Sheldon and Thoms (2006a)
	5. 1885	5. Reduced thalweg variability	5. Reich *et al.* (2009)
	6. 1962	6. Fine sediment deposition	6. Wilcock *et al.* (1996)
Riparian vegetation	1. 1954; 1988; 1949-1974; 1983; 1923-1979; Late 1800s	1.Vegetation encroachment into main channel	1. Auble and Scott (1998); Choi *et al.* (2005); Erskine *et al.* (1999); Gordon and Meentemeyer (2006); Kondolf and Batalla (2005); Kondolf *et al.* (1996)
	2. 1953	2. Reduced recruitment of riparian species	2. Scott *et al.* (1996)
	3. 1880s – 1950s	3. Reduced OM retention	3. Sheldon and Thoms (2006a)
	4. Late 1800s; 1962	4. Altered species composition	4. Kondolf *et al.*(1996); Merritt and Cooper (2000)
	5. 1951-1967	5. Reduced species richness and plant density	5. Nilsson *et al.* (1991)
	6. 1930s	6. Reduced species richness and increased plant density	6. Stromberg *et al.* (2007)
Connectivity	1. Review	1. Channel disconnected from floodplain	1. References in Kingsford (2000)
	2. Review	2. Reduced interchange with hyporheic zone	2. References in Boulton (2007) and Hancock (2002)
Water quality	1. 1900s	1.Increased nutrients	1. Camargo *et al.* (2004)
	2. 1885	2. Decreased N & P, increased dissolved O_2	2. Reich *et al.* (2009)
	3. Review	3. Decreased dissolved oxygen	3. References in Friedl and Wüest (2002)
	4. 1929	4. Altered nutrient dynamics	4. Ahearn *et al.* (2005)

Table 1.1 (continued) Examples of published studies of river regulation. Many impoundments impact on several ecosystem processes, with the earliest studies of dams built in the late 1800s.

Algae and biofilms	1. 1915-1968; 1920s	1.Increased algae	1. Nichols *et al.* (2006); Sheldon and Walker (1997)
	2. 1961	2.Dense periphyton growth	2. Voelz and Ward (1989)
	3. 1962	3. Reduced algal growth	3. Wootton *et al.* (1996)
	4. 1880s – 1930s	4. Different diatom taxa	4. Growns and Growns (2001)
Invertebrate communities	1. 1907-1974; 1953; 1966; 1970; 1963	1. Reduced diversity	1. Growns and Growns (2001); Jackson *et al.* (2007); Munn and Brusven (1991); Takao *et al.* (2007); Vinson(2001)
	2. 1907-1974; 1953; 1915 - 1968	2. Reduced EPT abundance	2. Growns and Growns (2001): Jackson *et al.* (2007); Marchant and Hehir (2002): Nichols *et al.* (2006)
	3. 1907-1974; 1966; 1915-1968	3. Increased tolerant taxa	3. Growns and Growns (2001); Marchant and Hehir (2002): Munn and Brusven (1991); Nichols *et al.* (2006)
	4. Review; 1980; 1905-1970	4. Fewer rheophilic taxa	4. Brittain and Saltveit (1989); Pardo *et al.* (1989); Ward and Garcia de Jalón (1991)

The impacts of flow regulation will also depend on the amount of associated land use change, which varies between studies and can often produce unpredicted effects (Friedl and Wüest 2002). Therefore, it is important to distinguish the effects of regulation from other anthropogenic changes (Brandt 2000). A realistic appraisal can not be made of the effectiveness of changes to management of the flow regime unless the direct effects of flow regulation can be distinguished from the confounding effects produced by subsequent land use changes.

As Grant *et al.* (2003) pointed out, there is a need for conceptual models which organise and synthesise this knowledge. Petts (1984) went some way towards this goal by proposing a three stage model of impoundment impacts, based on the influence of hydrology on sediment supply, consequent geomorphic changes, and biotic effects. Burke *et al.* (2009) used a three-stage approach to assess the 1st- and 2nd-order effects of regulated hydrology and channel hydraulics on riparian vegetation recruitment, while Naiman *et al.* (2000) added biological feedback mechanisms as a fourth dimension.

Grant *et al.* (2003) approached modelling from the perspective of geomorphology, suggesting that geology controls catchment-scale impacts, which then influence hydrology at the basin-scale. Naiman *et al.* (2005) used both the hydrological regime and position of the stream reach in the river catchment in an attempt to model the changes to riparian vegetation with flow regulation, while Bunn and Arthington (2002) proposed four principles to model the effects of different flow regimes on aquatic diversity. These concepts were combined in the ecological limits of hydrologic alteration (ELOHA) model (Poff *et al.* 2010), which uses the geomorphology and hydrology of individual streams to predict the effects of flow modification (Fig. 1.3).

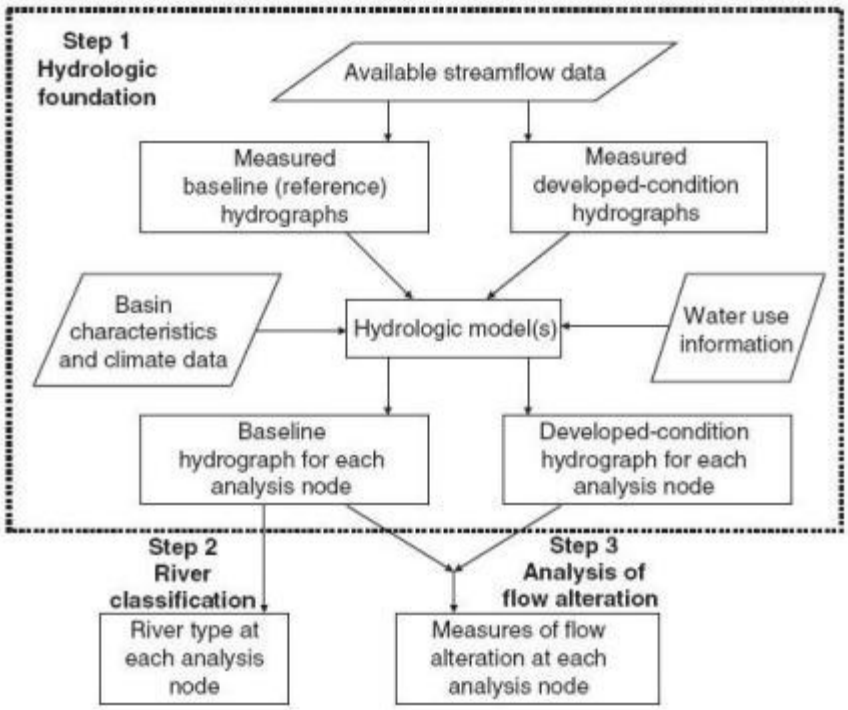


Fig. 1.3 The ELOHA frame-work uses three steps to develop a hydrologic framework for a river reach. Baseline conditions and predicted post-regulation alterations to the reference conditions are used to classify each stream reach and identify the alterations to the flow regime (Poff *et al.* 2010).

1.3 Aims and scope of this thesis

The overall aim of this thesis was to examine the long-term ecological effects of "anti-drought" flow regulation of a river in a cool temperate Mediterranean climate zone. Many factors can determine the presence

and abundance of biota in a river (Hynes 1970a). Consequently, rather than directly examining riverine fauna, the main focus of this study was on the availability and abundance of the basal resources which ultimately fuel the riverine food web. The macroinvertebrate community structure and their use of resources were also examined, to further understand the ecosystem effects of resource availability.

Lloyd *et al.* (2003) suggested that studies of many regulated rivers were flawed by the lack of appropriate reference sites, or the confounding effects of geology, reservoir stratification or land use. Smaller impoundments have been largely ignored in the published literature (e.g. Walker 1985; Baldwin *et al.* 2009) with the emphasis in reviews on recent high-impact impoundments. However, irrigation for agriculture comprises over 65% of water use worldwide, with over half the large dams constructed primarily for irrigation (WCD 2000). The majority of these are of short-term impoundments (Table 1.1), which are unlikely to predict the effects of long-term impoundment.

This study attempts to redress some of these issues by contrasting the regulated and unregulated branches of an eastern Tasmanian river system, where regulation for irrigation has been in place for over 170 years. Because the availability of resources is considered a major factor in aquatic invertebrate presence or absence (e.g.Wallace *et al.* 1997), and hence the abundance of higher level predators, particular emphasis was paid to riparian zone litter accession and benthic resources, and to the macroinvertebrate response to availability of these resources. While the pre-impoundment condition of the regulated Tooms River has not been quantified due to the age of the impoundment (1840), this study is unusual in that reference study sites were available on the adjacent, unregulated upper Macquarie River, with the same geology, riparian vegetation and land use, and there was little anthropogenic impact on Tooms River beyond regulation. Moreover, Tooms Lake is shallow, so does not stratify (Croome and Tyler 1972) to create the water temperature

differences which confound many regulation studies (e.g. Angradi 1994). On this basis, the differences in ecological response measures between the rivers can be strongly linked to modification of the flow regime.

Poff *et al.* (2010) considered that there was a lack of studies on the impacts of flow regulation on riparian productivity and in-stream retention. This thesis adds to the knowledge base, concentrating on some of the impacts of river regulation for irrigation or water conservation, and generally follows Petts' (1984) proposal of successional impacts, while integrating the appropriate aspects of the ELOHA principles. In contrast to ELOHA, which uses recent data to predict future impacts of flow alteration, historical flow records have been used to examine the differences in the flow regime between the two rivers, and consider the impact of that regime on ecosystem variables.

The original study design was event-based, with some sampling protocols designed to cover high flow events and articulated with the TEFlows project (DPIPWE 2010). The sampling programme was subsequently reoriented to take advantage of the "supra-seasonal drought" (Lake 2003) which coincided with the 3 years of fieldwork in this study. This provided an unique opportunity to examine whether any differences between the Macquarie and Tooms Rivers diminished under the influence of low flows in each river, particularly as higher irrigation demands are likely to exacerbate future low flows.

The unusually low flows in Tooms River were expected to influence algae and biofilms abundance, and potentially impact on litter accession to the benthos, with reduced connectivity between the riparian zone and wetted channel. As a result, it was hypothesised that there would be a convergence of aquatic biota towards a common species assemblage, more typical of slow-flowing habitats.

1.4 Thesis structure

Chapter 2 describes the climate and hydrology of the two rivers (frequency, magnitude and seasonality of flow events) and the second-order impacts (Petts 1984) of the modified flow regime on channel geomorphology and the riparian vegetation at each study site. Chapter 3 explores the influence of the riparian vegetation on riparian litter dynamics at each site. Artificial turf mats were used to monitor patterns of riparian litter over 2 years, while cellulose decomposition potential assessed the influence of decomposition on litter accumulation.

Chapter 4 examines the influence of the riparian vegetation structure on allochthonous and autochthonous benthic resources, which was tested with a quarterly monitoring programme at each study site, laboratory trials of leaf buoyancy and a field study of cellulose decomposition. Because water quality differed between the rivers, suspended sediments and nutrients were examined to support interpretation of the differences between the regulated and unregulated rivers.

The third-order impact of flow regulation and the additional impact of the drought on the macroinvertebrate community structure were explored with quarterly collections of macroinvertebrates from each river (Chapter 5). Chapter 6 examines the use of allochthonous and autochthonous resources by the benthic food web, with field and laboratory trials. Stable carbon and nitrogen isotopes were used to analyse macroinvertebrate diets over 2 years (Ch. 6.1), and laboratory feeding preference trials examined and corroborated the stable isotope results (Ch. 6.2). Chapters 6.1 and 6.2 have been submitted for publication and have been formatted to comply with the requirements of the individual journals. There is some duplication of information from previous chapters, particularly in the introductions and methods sections.

Chapter 7 is a synthesis and discussion of the results in the context of the regulation of Tooms River and the drought on both rivers, and proposes a

conceptual model of the interactions between the flow regime and the measured ecosystem variables. This is intended to inform water managers of the likely consequences of long-term impoundment of similar forested rivers in Mediterranean climate zones and proposes some mitigation measures.

Chapter 2 The influence of river hydrology on channel morphology and site characteristics

2.1 Abstract

A river's flow regime (hydrology) influences its geomorphology, with consequent impact on the structure of the riparian vegetation and instream resource availability. This chapter examines the 1st- and 2nd- order effects of flow regulation, by contrasting upstream and downstream sites on the regulated Tooms River and unregulated Macquarie River in eastern Tasmania. The climate of the catchment is discussed and the study sites introduced. A range of flow metrics were used to analyse the hydrology of the two rivers. Tooms River has a stable, but seasonally reversed flow regime, with few floods and no zero flow periods. The unregulated Macquarie River has a highly variable flow regime, with irregular but powerful floods and frequent cease to flow periods. The river planform was surveyed at each site to examine the influence of the flow regime on the geomorphology. The stable flow regime in Tooms River has produced an incised channel, with mature trees close to the waters edge, whereas the Macquarie River has a defined riparian zone with vegetation distinct from the surrounding woodland.

2.2 Introduction

Under a natural flow regime, the channel form is produced by the downstream movement of sediments. The river loses kinetic energy, or erosional power with sediment transport, with turbulence, or with friction with the substrate, stream banks or riparian vegetation. Damming a river can remove or reduce sediment flow, increasing the kinetic energy of the water (Kondolf 1997). This can influence the geomorphology of the channel and banks, either eroding or depositing sediments, with consequences for aquatic and riparian vegetation (e.g. Nilsson and Berggren 2000). The hydrology of a river acts on and with the channel morphology to influence sediment and nutrient transport, habitat availability for aquatic biota, and the presence and abundance of food resources (Petts 1984).

This chapter introduces the climate and physical characteristics of the study sites, and examines the hydrology and geomorphology of the two rivers. These factors set the scene for the following chapters, which explore the influence of the different flow regimes on riparian vegetation dynamics, benthic resources and macroinvertebrate communities.

2.3 Study design

The Macquarie River, in eastern Tasmania, rises in the Eastern Tiers, just south of Lake Leake, at an elevation of 575 m. It has a total length of about 180 km, and a total catchment of 4 241 km^2 (DPIW 2008). This study examines the headwaters of the Macquarie River, with a total length of about 40 km, upstream of the junction with Tooms River. Tooms River is a regulated tributary of the Macquarie, rising at an elevation of 463.5 m, with a total pre-impoundment length of about 25 km and catchment of approximately 80 km^2 (Croome and Tyler 1972) (Table 2.1). The two Macquarie River sites were chosen on the basis that they have been classified as having high naturalness (CFEV 2005) and represent genuine reference conditions for each of the Tooms River sites (sensu Stoddard *et al.* 2006).

While the headwaters of Tooms River have been heavily modified by the impoundment, Stoddard *et al.'s* (2006) 'minimally disturbed' category can be applied to the upstream Macquarie site, which has had no modification from what would have been the pre-European settlement (1803) state of Tooms River. The two downstream sites, in contrast, have both been modified by low-impact agriculture, primarily year-round low density sheep grazing (< $0.5.ha^{-1}$). The major physical difference between these sites is the regulation of the flow regime in Tooms River.

Table 2.1 Location and physical characteristics of each study site. Base data from CFEV© and The List, © State of Tasmania, and field measurements.

	Macquarie River		Tooms River	
Site variables	Upstream site CB	Downstream site IF	Upstream site TL	Downstream site BB
Latitude	42°09'2.97"S	42°09'51.03"S	42°12'41.70"S	42°11'31.69"S
Longitude	147°49'59.04"E	147°42'43.73"E	147°46'21.07"E	147°43'50.60"E
Catchment area (km^2)	85. 9	169.3	62.3	75.6
Orientation	ENE-WSW	E-W	ENE-WSW	SSE-NNW
Discharge ($m^2.sec^{-1}$)	0 - 130	0 – 131.3	0.002 – 22.4	0.002 – 22.6
Mean annual runoff ($ML.y^{-1}$)	23669.40	41499.71	13860.94	15780.16
Altitude (m)	408	290	448	282
Mean bankful width (m)	8.9	5.1	2.8	5.5

2.4 Study sites

Two sites were selected on each of the upper Macquarie and Tooms Rivers, paired by one site in the headwaters of each river and a second site in the downstream alluvial valleys (Fig. 2.1). Potential study sites were limited by the availability of access, but were chosen to be as comparable as possible in terms of the key features of adjacent vegetation, land use, geomorphology and in-stream substrate. The upstream Tooms River site, "Tooms Lake" (TL), was within the lakeside water reserve, approximately 1 km downstream of the dam. The downstream Tooms site, "Blanket Bottom" (BB), was just above the junction with the Macquarie River and was selected as the most distant reach from the dam and therefore the most likely to show recovery from impoundment. The upstream Macquarie River site, "Colonels Bridge" (CB), was far enough from the headwaters to have perennial flow, had unmodified riparian vegetation and access from an abandoned forestry road. The downstream Macquarie site, "Island Flats" (IF), was close to the junction with Tooms River, was readily accessible and provided an unregulated comparison with the downstream Tooms site, which had a similar grazing history. The understory of each downstream site had a mixture of introduced and native grasses and rough grazing land. Agricultural activity was predominantly low density (< 0.5. ha^{-1}) dryland sheep grazing for wool production.

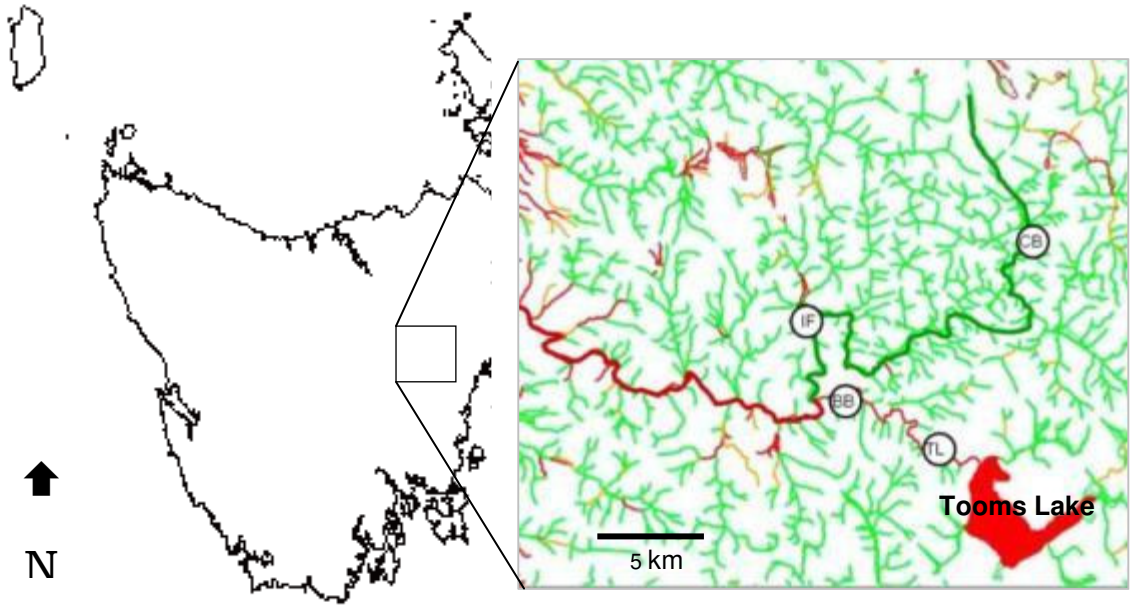


Fig. 2.1 Location of study sites, where CB and IF are the upstream and downstream Macquarie sites, and TL and BB are the upstream and downstream Tooms sites, respectively. The upper Macquarie River is shown in dark green. Tooms River is in red, connecting Tooms Lake with the lower Macquarie in bold dark red. The colours indicate the naturalness of the river reaches, with high naturalness shown in green and low naturalness shown in red. Orange indicates moderate naturalness. Most minor tributaries are shown in light green. Map modified from base data by CFEV and the LIST, © State of Tasmania.

All sites have similar geology, dominated by Jurassic dolerite with some Triassic sandstones (Jerie *et al.* 2003b) and satisfy Ward and Stanford's (1995b) definition of a 'mountain headwater reach' (Fig.1.1). Both rivers are bedrock controlled, with the constrained channels diverted by dolerite intrusions. In common with many rivers of east coast Tasmania, the Macquarie River responds rapidly to rainfall events, resulting in a highly variable (or 'flashy') flow regime (DPIPWE 2010). This is likely to have been the original condition for the present Tooms River.

The original Toombs Marsh was first dammed in 1840 as a secure water supply for farmer-settlers in the Ross area (Croome and Tyler 1972; Mason-Cox 1993). The dam failed to fill in the first winter, but was destroyed by floods in the second year and again in 1863 and 1900

(Mason-Cox 1993), demonstrating the flashy flow regime. Tooms Lake currently has an area of approximately 6 km^2, a mean depth of 3.6 m and volume of 24 000 ML. The earth-filled dam has been approximately 4 m high since at least 1864, with a concrete spillway (DPIW 2008). Water is released from the dam via a sluice gate at the base of the dam wall (Fig. 2.2), which supplies irrigation for downstream agriculture and domestic water supply for the town of Ross, under the management of the Elizabeth Macquarie Irrigation Trust. Water is released from the dam in summer and other times of low flow, to augment flows in the Macquarie River. There is an environmental flow requirement of 4.1 $ML.day^{-1}$ at Fosterville, over 50 km downstream of the Tooms River - Macquarie River junction and upstream of the Elizabeth River junction with the Macquarie (DPIW 2008).

Fig. 2.2 Tooms River outlet in the Tooms Lake dam wall in February 2008, with discharge recorded as 0.18 $m^3.sec^{-1}$ by the downstream gauge.

2.5 Catchment climate

The Macquarie catchment has a cool temperate climate, with low to medium rainfall restricted by mountain ranges to the west and east of the catchment (Fig. 2.3).

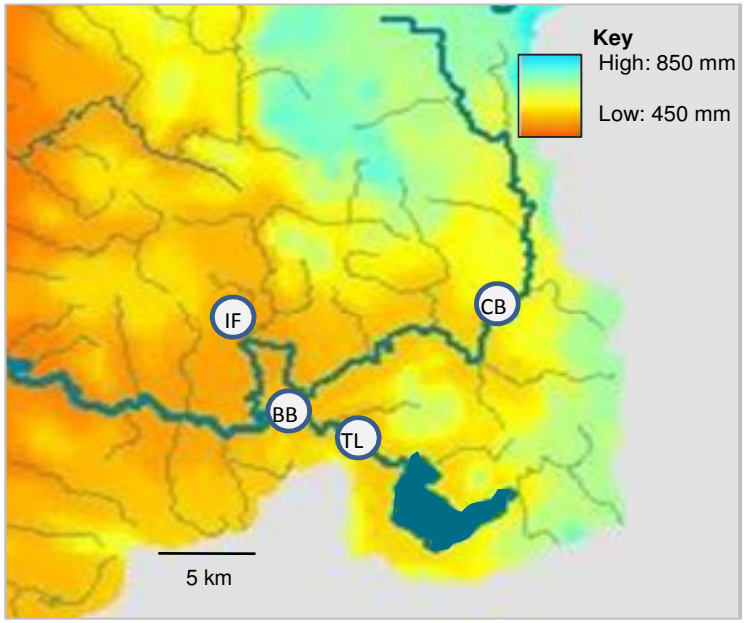


Fig. 2.3 Mean annual rainfall (mm) distribution across the upper Macquarie catchment. The driest areas are indicated by red tones, blue tones indicate the highest rainfall areas. The major rivers and Tooms Lake are shown in dark blue. Figure modified from DPIW (2008).

Although the maximum temperature rarely exceeds 30° C, the average annual rainfall of 520 mm is in deficit to annual evaporation of about 1000 mm p.a. (Bureau of Meteorology 2010) (Fig. 2.4).

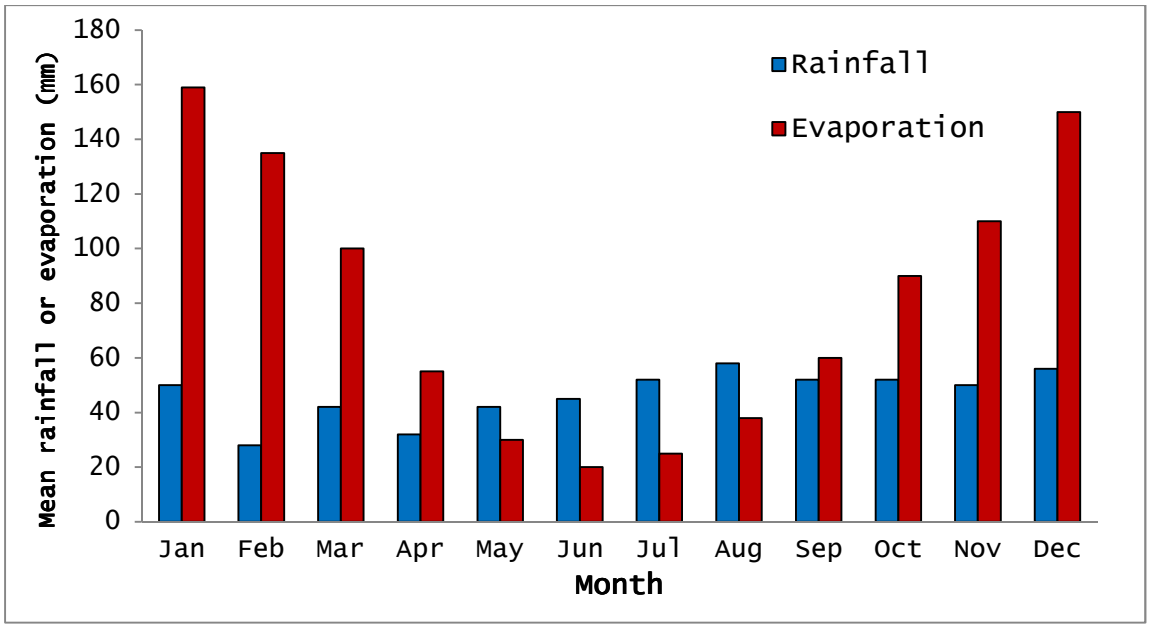


Fig.2.4 Mean monthly rainfall and pan evaporation (mm) for the upper Macquarie catchment 1970 – 2008 (modified from DPIW (2008)).

Rainfall is fairly evenly spread throughout the year (Fig. 2.4), with lowest rainfall in late summer and highest rainfall in spring, although heavy rain can be directed into the catchment in any season when a low pressure system forms off the east coast (Bureau of Meteorology 2010). Rainfall was assumed to be similar across the study sites, although there can be high within-catchment rainfall variation in eastern Australia (Croke and Jakeman 2001). Incomplete precipitation records were available from rain gauges at Tooms Lake and Mt Morriston, approximately 13 km downstream of the study sites. Missing data were replaced with data directly interpolated from gauges at Lake Leake, 15 km north of the study sites, Swansea 15 km to the east and Ross, approximately 25 km to the west.

Rainfall during 2006 – 2008 was the lowest in recorded history for eastern Tasmania (Fig. 2.5), with total precipitation for this area only 1050 mm during this period (Bureau of Meteorology 2010).

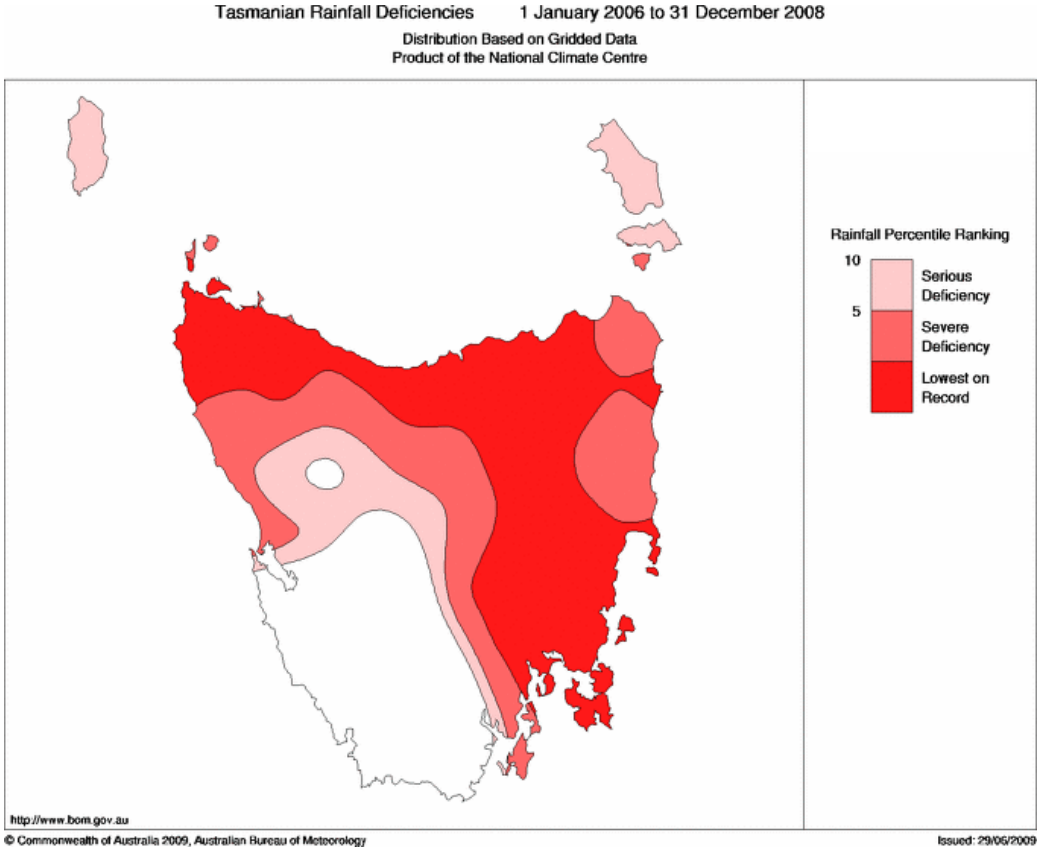


Fig. 2.5 Rainfall deficiency for Tasmania during the 2006-2008 study period. Map produced by the National Climate Centre (NCC 2009). Darker colours indicate higher severity of rainfall deficit, with lowest rainfall on record shown in red. Average rainfall conditions were experienced in areas without colour.

The upper Macquarie River flowed intermittently through 2006 – 2007, but ceased to flow between December 2007 and November 2008. Over this period, the upstream Macquarie site, CB, was reduced to small groundwater-fed pools, whilst the downstream site, IF, dried out completely. In contrast, continuous low flow was maintained in Tooms River to augment the lower Macquarie River. Although abstraction for irrigation is prohibited when the Tooms Lake storage falls below 9 000 ML, discharge was maintained at minimal levels to satisfy environmental flow requirements (DPIW 2008).

2.6 Hydrology

2.6.1 Methods

Changes to the hydrological regime impact on sediment and nutrient transport to produce first-order regulation effects (Petts 1984). River hydrology for this study was derived from data published online (WIST 2010), which showed records from a stream gauge immediately below Tooms Lake; a discontinued gauge at Longmarsh, approximately 1 km upstream of the Macquarie River sites; and a gauge at Trefusis, approximately 12 km downstream of the Tooms - Macquarie junction. The gauge at Trefusis replaced the flow gauge at Longmarsh in 1990.

The variability of flow in the two rivers was examined with selected metrics devised by Puckridge *et al.* (1998) and employed by Growns and Marsh (2000) in the analysis of the hydrology of southeastern Australian streams. Puckridge *et al.* (1998) recommended using data series of at least 15 years to calculate flow metrics. Initially, flow for the two Macquarie sites for the period 1970 – 2009 was calculated with a rainfall-runoff model. However, this data set was considered unreliable because the model did not detect the observed or recorded cease-to-flow periods in this river. Models are recognised as poorly representing low flow periods (Smakhtin 2001), and downstream gauges may not reflect the conditions in the upper catchment (Niadas 2005).

Comparable gauged data were available for both rivers for the period May 1975 – October 1990 from the Tooms River and Longmarsh gauges, which satisfied Puckridge *et al.*'s (1998) criterion. Mean, median, minimum and maximum discharges for the Macquarie River (Table 2.1) were calculated from the Longmarsh and Tooms gauge records for the full 15 year data set. Additional flow metrics were calculated from the available gauged data, using the formulae in Microsoft Excel 2007 (Growns and Marsh 2000) (Table 2.2). Where values were missing from one data set, the value

for that day was excluded from both data sets. This constituted less than 0.4% of the total values.

Because annual rainfall in eastern Tasmania has declined since 1990 (Bureau of Meteorology 2010), an additional data set was generated for the ungauged Macquarie River for the period 2000 – 2009. This was calculated by subtracting the mean daily flows recorded by the gauge at Tooms Lake, from mean daily flows recorded at Trefusis on the downstream Macquarie River. The data were corrected for the time lag between recording stations (12 h), and for input from minor tributaries with recorded historic mean daily flows from the discontinued gauging weir at Longmarsh. The adjusted 2000 – 2009 data were used to plot a time series of mean daily flow and to calculate flow frequency curves. Data were plotted using the *ggplot2* package (Wickham 2009) in R version 2.11.0 (R Development Core Team 2010). Analysis of variance (ANOVA) examined the strength of the variation between rivers.

Flow metrics were calculated for each river, rather than for individual sites, because there were no major tributaries between upstream and downstream sites on each river to significantly modify the flow. Water abstraction for irrigation was prohibited for much of the study period, reducing releases from Tooms Lake, although some flow was maintained to meet downstream environmental flow allocations. However, the property adjacent to the downstream Macquarie River site has licensed water rights (DPIW 2008) and is likely to abstract water from the upstream broadwater pool, reducing flow at this site. There are also likely to be unmetered water abstractions from the Macquarie River between Tooms River and the Trefusis gauge.

2.6.2 Results

The establishment of hydrological metrics was recommended by Poff *et al.* (2010) as the first stage in determining the impact of flow regulation on ecological variables. The Macquarie River has a highly variable flow regime, with frequent periods of low or zero flow. Lowest flows are typically in summer, but can occur at any time of the year (Fig. 2.6). The drought period of 2006 – 2008 produced very low discharge, with 412 zero flow days (37.6%) during this period. In contrast, figure 2.6 shows that high and low flows were seasonally reversed in Tooms River. Lowest flows were in winter, but the river was never completely dry. High flows were rare and restricted to periods of high rainfall when the full dam spilled.

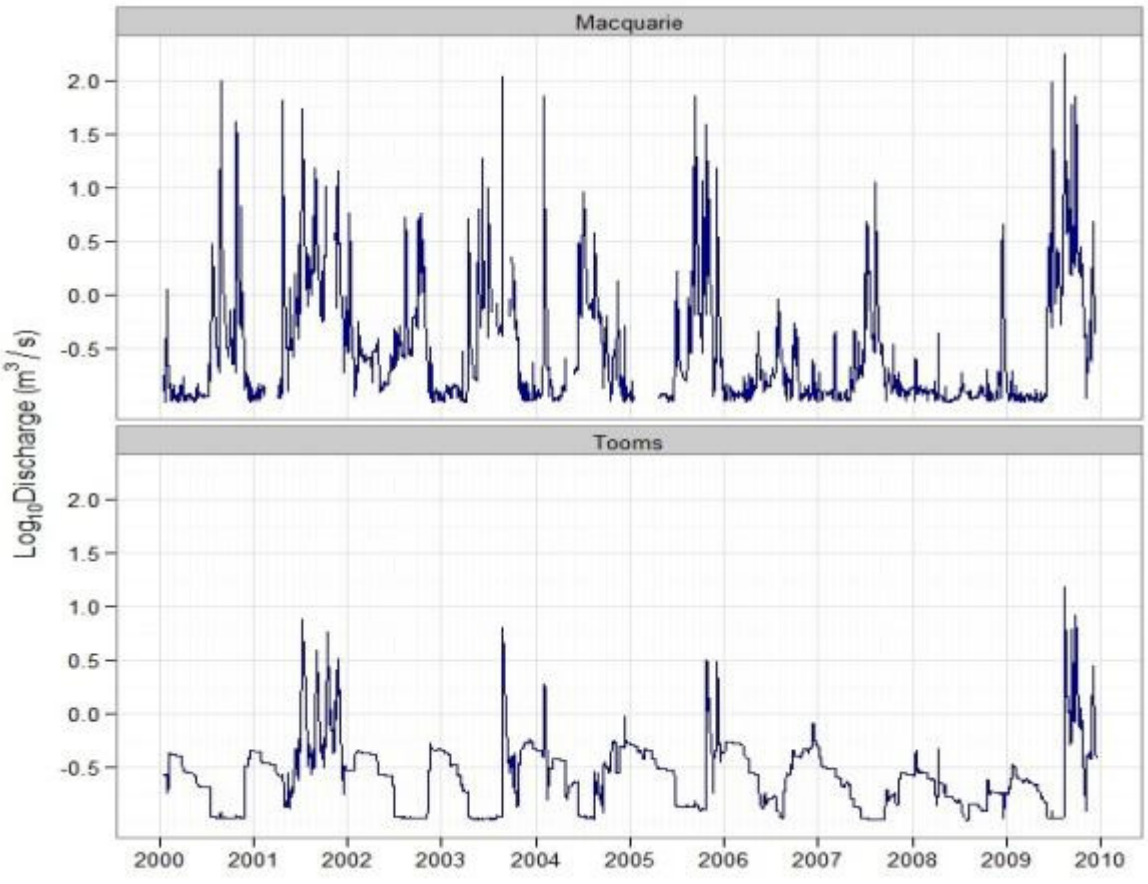


Fig. 2.6 Variation in mean daily discharge for the Macquarie (upper panel) and Tooms (lower panel) Rivers for 2000 – 2009, with the height of the bars indicating discharge ($m^3.sec^{-1}$) on a logarithmic (base 10) scale and date (year) on the x-axis.

Analysis of flow frequency from 2000-2009 shows that mean daily discharge in both rivers equaled or exceeded 0.01 $m^3.sec^{-1}$ (cumecs) for 80% of the time. However, Tooms River did not have the rare high flows shown for the Macquarie River, but had more flow at the low discharge end of the scale. Sixty percent of the time discharge was 0.1 cumecs in Tooms, but less than 0.05 cumecs in the Macquarie (Fig. 2.7).

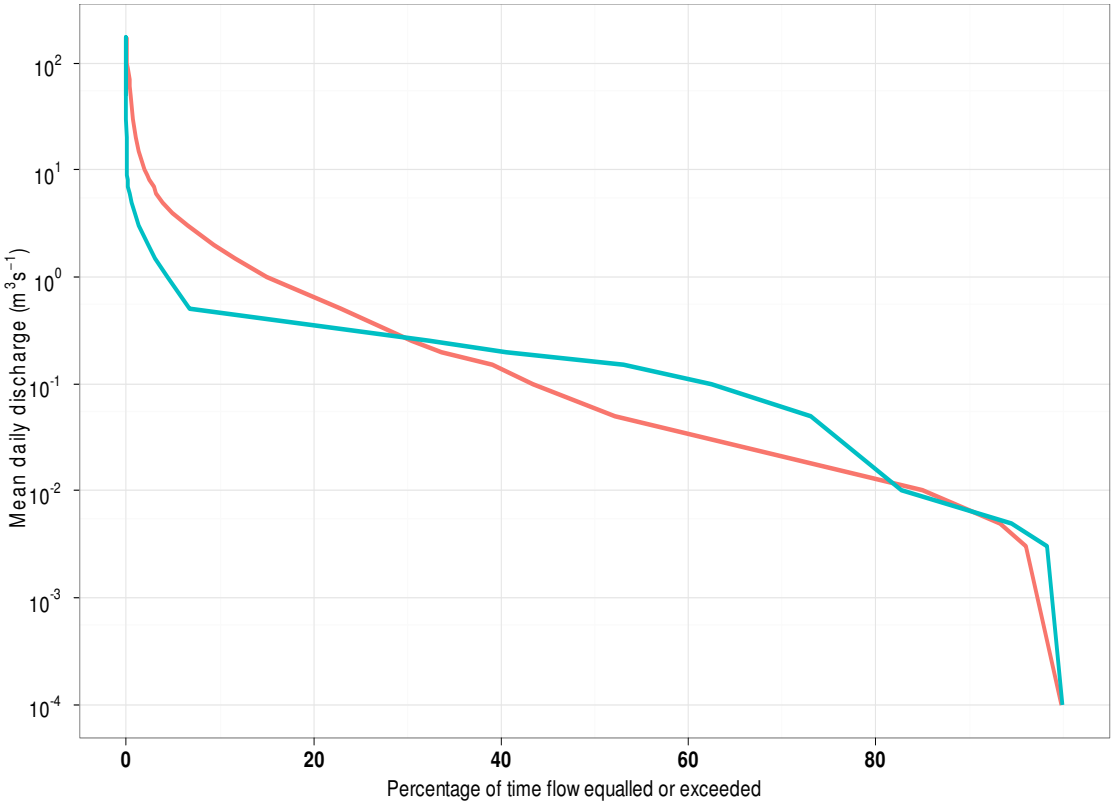


Fig. 2.7 Flow frequency as $\log_{10}$ modelled mean daily discharge ($m^3.sec^{-1}$) for the Macquarie (red) and Tooms (blue) Rivers, where the lines indicate the percentage of time that the flow was equal to, or higher than the discharge shown on the y-axis, in the decade between 2000 and 2009.

There is an abrupt shift in the low frequency zone for Tooms River, where infrequent floods occur as the dam spills, and another abrupt shift for both rivers in the high frequency region (Fig. 2.7). The low frequency of high flows in the Macquarie River is indicative of the effects of heavy rain in a small catchment, while the abrupt change to the high frequency of

low flow is indicative of the intermittency of the Macquarie River, and long periods of very low flow in Tooms River. Tooms River discharge was significantly lower and less variable in winter 2007 than in winter 2006 (ANOVA, $F_{(1, 184)} = 94.53$, $p < 0.0001$). Discharge was also significantly lower in the summer irrigation period 1 November 2007 – 31 March 2008 than in the same period for 2006 - 2007 ($F_{(1, 263)} = 132.03$, $p < 0.0001$).

The long, flat curve for Tooms River (Fig. 2.7) shows that flow regulation maintains moderate flows for most of the year (DPIW 2008). Median discharge (Q_{50}), calculated from gauged 1975-1990 data, was higher in Tooms River than in the Macquarie River (Table 2.2), while minimum flow (Q_{90}) in Tooms River was 0.1 $m^3.sec^{-1}$ and zero in the Macquarie. Analysis of flow-duration indices shows that base flow (Q_{90}/Q_{50}) contributed a greater proportion of the flow in Tooms River (Gordon *et al.* 1992), indicating the maintenance of low flows typical of regulated rivers (McMahon and Finlayson 2003), while the flood peak (Q_{10}/Q_{50}) was almost twice as high in the Macquarie River. The maximum flow (Q_{max}) was almost 6 times higher in the Macquarie, but discharges higher than 85 $m^3.sec^{-1}$ were only recorded twice in the 15 year period, while there was zero flow for up to 170 days per year (mean of 56 days). February and March were the driest months, with the Macquarie River completely dry for eight of the fifteen Februarys. The longest period without flow in this data series was from December 1983 to mid-June 1984, although the river was dry for 10 months in 2008. The coefficient of variability (CV) and flow variability character (Puckridge *et al.* 1998) of the Macquarie River were significantly higher than the values for Tooms River, indicating much greater variability of flow.

Table 2.2 Flow-duration analysis of the Macquarie and Tooms Rivers, based on gauged flows for 1975-1990. The variable Q represents discharge, where Q_{10} = is the 90th percentile value and the discharge that is exceeded 10% of the time. Metrics are expressed in $m^3.sec.^{-1}$, except for the coefficient of variation (CV)*, which is dimensionless.

Flow metric	Flow variable	Macquarie River $m^3.sec^{-1}$	Tooms River $m^3.sec^{-1}$
Q_{min}	Minimum flow	0	0.002
Q_{max}	Maximum flow	130.59	22.40
Q_{10}	High flow index	1.85	1.04
Q_{50}	Median flow	0.13	0.30
Q_{90}	Low flow index	0	0.01
Q_{90} / Q_{50}	Base flow index	0	0.04
Q_{10} / Q_{50}	Flood peak	14.37	3.51
$(Q_{10} - Q_{90}) / Q_{50}$	Flow variability	14.37	3.46
Std.dev. flow values / mean flow	Coefficient of variation (CV)*	4.33	2.35
Mean/median	Skewness of flow	7.02	1.96

Because the base flow value (Q_{90}) for the Macquarie River is zero, the flood peak and flow variability indices for this river are identical. Indices of flow variability are calculated against median discharge, while the CV is calculated against mean discharge. The value for skewness of flow indicates the extent to which the mean value deviates from the median value, with a higher value indicating greater flow variation (Growns and Marsh 2000).

2.6.3 Discussion

Walker (1985) claimed that Tasmanian rivers were hydrologically distinct from mainland Australian rivers, due to mountainous terrain and high rainfall. Several other publications use average Tasmanian rainfall to classify the state's river flows (e.g. DPIE 1987). However, Tasmania has a strong west-east rainfall gradient (Langford 1965), so that the Macquarie River system in the central east is more typical of many south-eastern Australian rivers than of a typical Tasmanian river, with low rainfall and seasonally intermittent flow. Kennard *et al.* (2010) classified the Macquarie River as "baseflow perennial", in common with eastern

Victorian and northern NSW coastal rivers. However, this classification was based on flow records from the gauge at Trefusis (see section 2.5.1), so was heavily influenced by the regulated flow regime. In contrast to the published classifications of this river (e.g. Kennard *et al.* 2010), the Macquarie River should be classified as "intermittent runoff" using Poff's (1996) river classification criteria, according to the flow metrics reported in this chapter, and is therefore typical of many rivers in semi-arid areas of Australia.

2.7 Hydraulic modelling

Hydraulic models were developed for all sites with HEC-RAS 4.0.0 software (Hydrologic Engineering Center 2008) to assess the second order impact of the hydrologic regime on the channel morphology (Petts 1984). Surveyed contours were used to construct a channel profile for each study reach, which allowed modelling of the extent of measured or historic flow levels. Nine to 14 transects were surveyed at each site, to the upper edge of the historic river channels, within the limits of sightlines. Intermediate transects were interpolated by HEC-RAS where the program could not connect steady flow between surveyed transects. The Macquarie River sites were surveyed with a dumpy level and staff. The Tooms River sites were surveyed at a later date with a Total Station (Leica Geosystems AG, Heerbrugg, Switzerland) and prism. By convention, the right bank is taken as looking downstream. The Macquarie sites were completely dry during the survey, so the model was calibrated by comparing modelled and observed water surface heights for discharge measured on a single sampling occasion. Three-dimensional profile plots of active channel and bankful discharges were constructed to examine inundation patterns at each site.

2.7.1 Macquarie River sites

Although Hamlet *et al.* (2005) define the upstream Macquarie site, CB, as part of a gorge sequence, the river flows through a broad constrained

channel, probably a result of prehistoric flows (Jerie *et al.* 2003a) (Fig. 2.8). Bedrock and large boulders intersperse with shallow pools (< 1.0 m deep). The right bank has a much steeper gradient than the left bank, which forms a narrow floodplain.

The channel at the downstream Macquarie site, IF, is incised and confined where flow is constricted by a bridge at the top of the reach (Fig. 2.9). A pool (~ 750 mm deep) has formed below this constriction. The bottom of the reach is characterised by low gradient. The right bank is a flat floodplain extending to Punch's Marsh. Water is channelled into a secondary channel on the left bank at moderate flows (~1.3 cumecs).

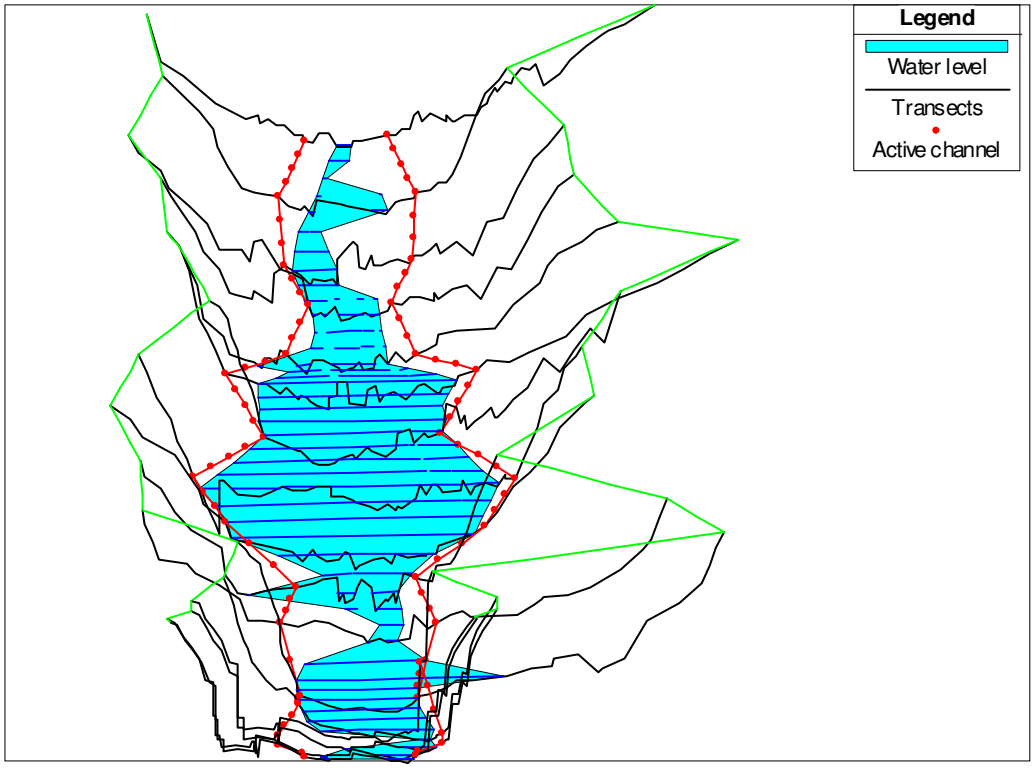


Fig. 2.8 The *x-y-z* profile at base flow (0.01 cumecs) of the upstream Macquarie River site Colonels Bridge (CB). The river flows from top to bottom of the panel. The active channel bank stations are shown by the red lines, with surveyed transects in black, and the water level indicated in blue.

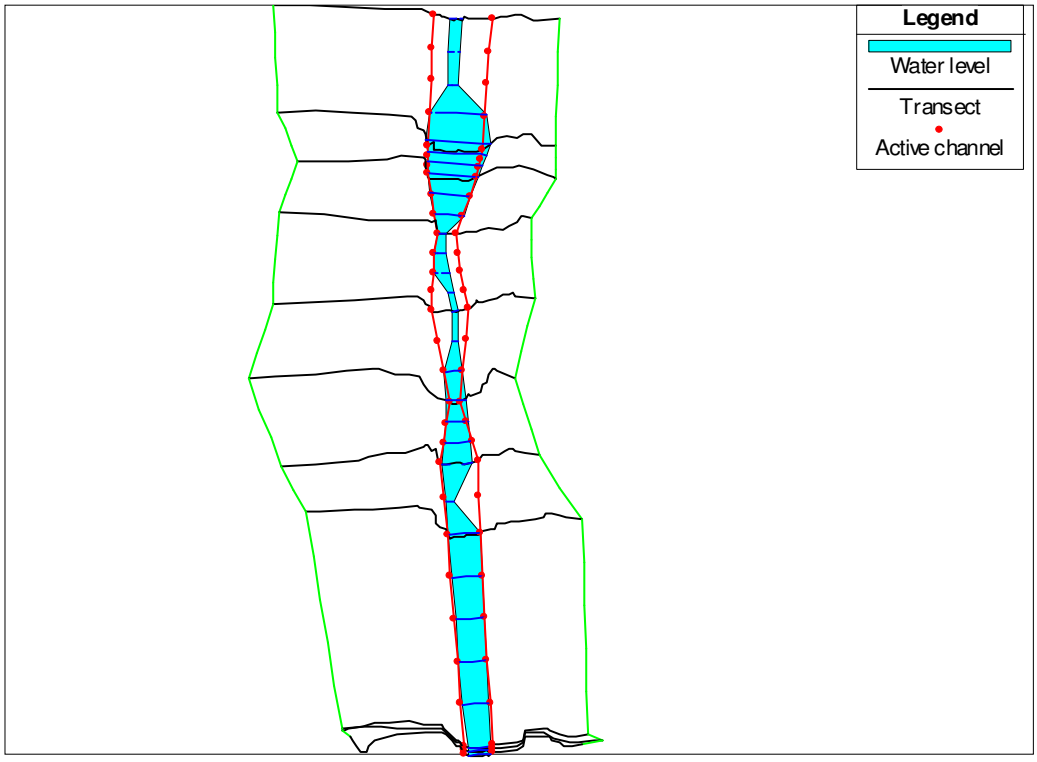
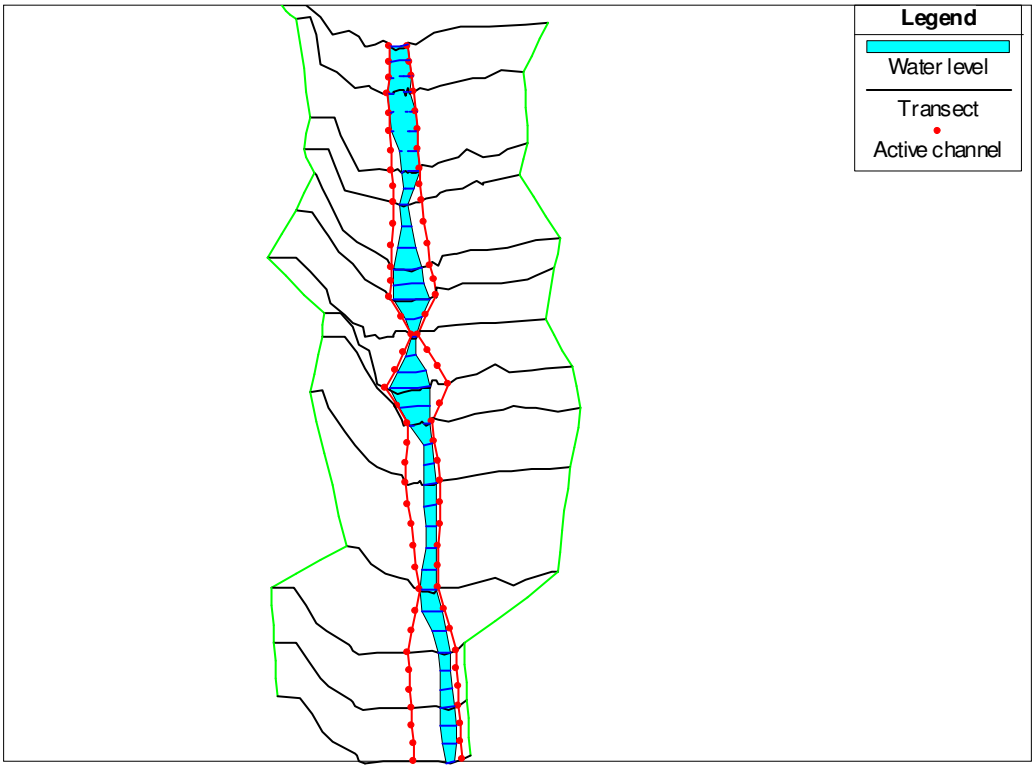


Fig. 2.9 The *x-y-z* profile at base flow (0.01 cumecs) of the downstream Macquarie River site Island Flats (IF). The river flows from top to bottom of the panel. The active channel bank stations are shown by the red lines, with surveyed transects in black, and the water level indicated in blue.

2.7.2 Tooms River sites

Surveyed transects at the upstream Tooms site, TL, show channel contraction, with bedrock intrusions constricting flow (upper panel, Fig.2.10). The right bank has been terraced by historic flows, with a relatively level depositional zone on the left bank.

The downstream Tooms study reach (BB) has pools (up to 1.5 m deep) interspersed with riffles and some bedrock constriction (lower panel, Fig.2.10). Historic river terraces are well developed on the left bank, particularly towards the bottom of the reach. Large boulders are more prevalent in the channel than at the upstream site.



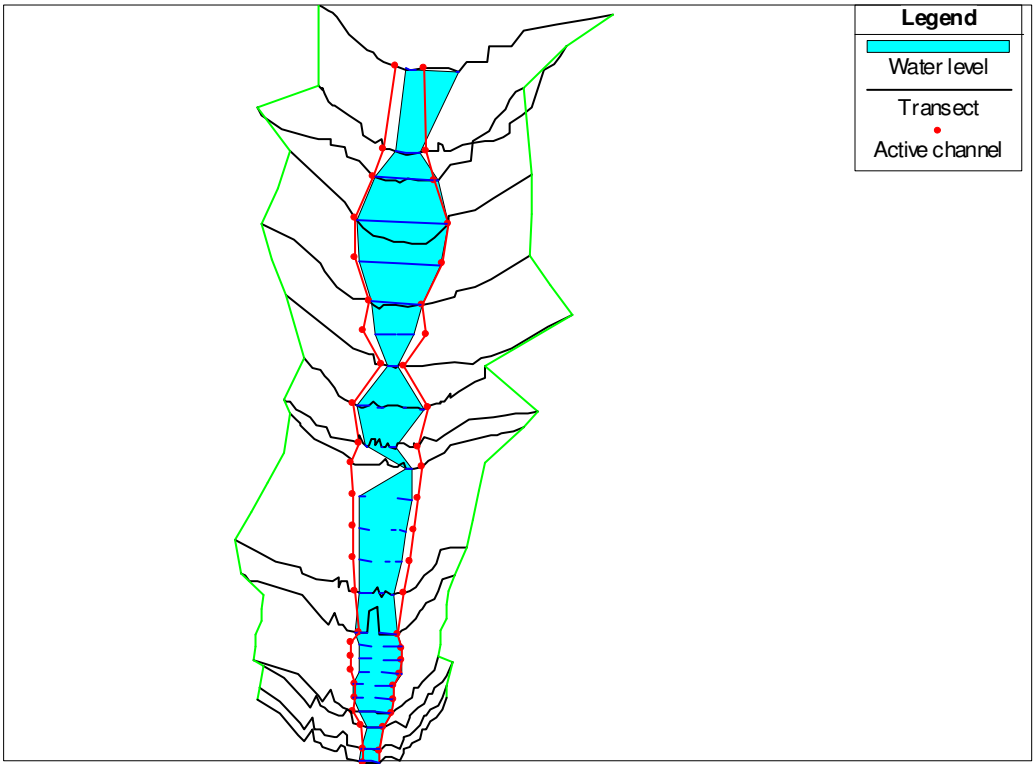


Fig. 2.10 The upper panel shows the *x-y-z* profile at base flow (0.01 cumecs) of the upstream Tooms River site Tooms Lake (TL). The lower panel shows the downstream site Blanket Bottom (BB). The river flows from top to bottom of each panel. The active channel bank stations are shown by the red lines, with surveyed transects in black, and the water level indicated in blue.

2.8 Vegetation and site descriptions

The second-order effects of regulation (Petts 1984) focus on channel form and alterations to the riparian zone, and the resulting impacts on primary productivity. The strength of these effects will depend on and influence individual site conditions. Where the stream bed is dominated by bedrock, regulation effects may be indicated by the riparian vegetation structure (Nichols *et al.* 2006). Dunne and Leopold (1978) proposed that channel form would be controlled by one in 50 year floods, but one in two year floods would control riparian vegetation dynamics. Stanley *et al.* (1997) suggested that the bed morphology would influence different patterns of drying in different sections of streams. Each of the sites in the current study had unique factors which may impact on the measured ecosystem variables.

2.8.1 Macquarie River sites

The upstream site on the Macquarie River (CB) is in State Forest close to the Colonels Hills, 1 km downstream of the disused Longmarsh gauging weir and upstream of the bulwarks of a dismantled bridge. Elevation contours on the map (Fig. 2.11) illustrate the presence of downstream pools.

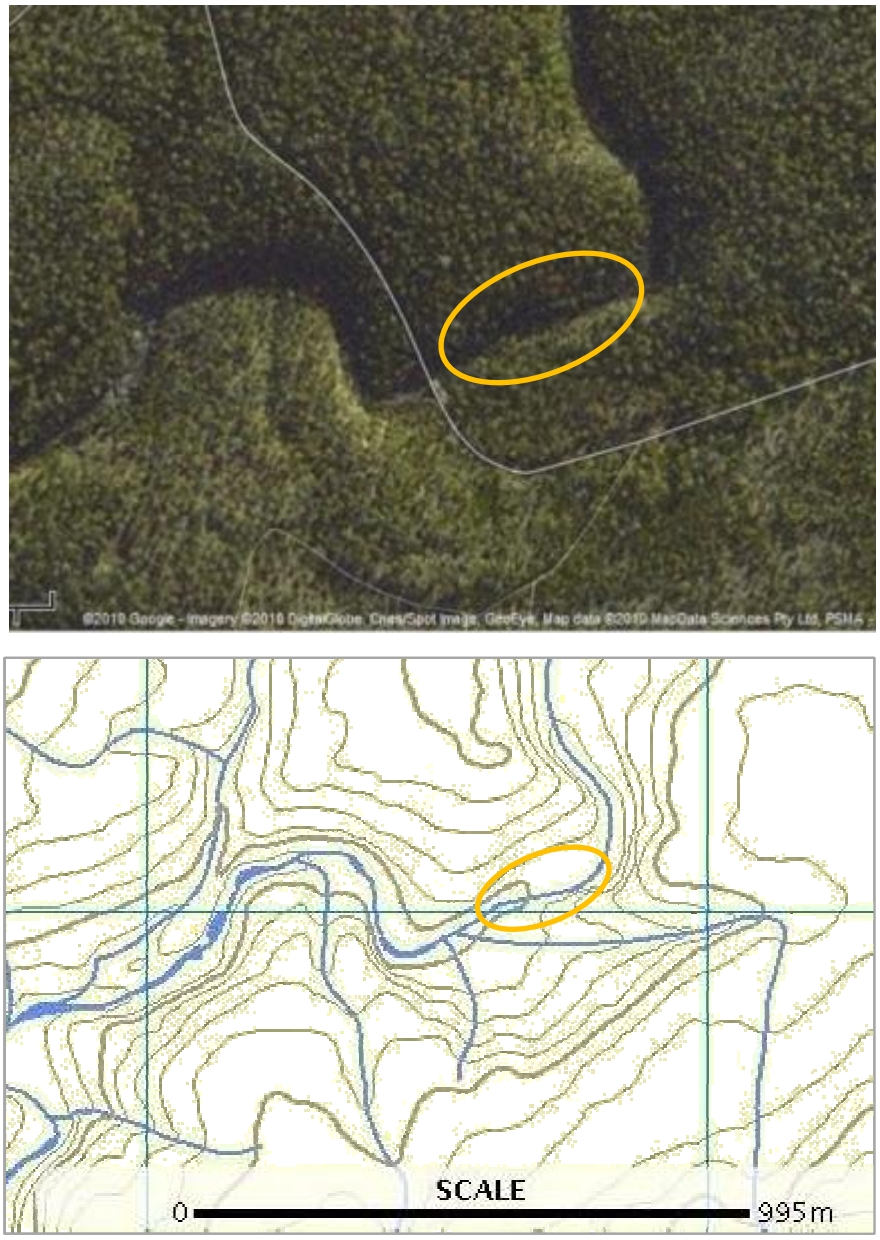


Fig. 2.11 Satellite image of the upstream Macquarie River site CB (upper panel). The river flows top to bottom left of the photo (Google Maps, 2010). The lower panel is a topographic contour map, with contours at 10 m intervals in grey and the river and minor and ephemeral tributaries in blue. The study site is outlined in yellow (modified from The List (2009)).

The vegetation is essentially natural, with mature eucalypts set back from the river edge, and a dense riparian band of mainly *Leptospermum lanigerum* and *Acacia mucronata* (Fig. 2.12). The stream substrate is an unsorted mixture of pebbles, cobbles, boulders and bedrock. The river profile demonstrates the narrow channel at base flow, and the extent of 2 year and 5 year frequency floods.

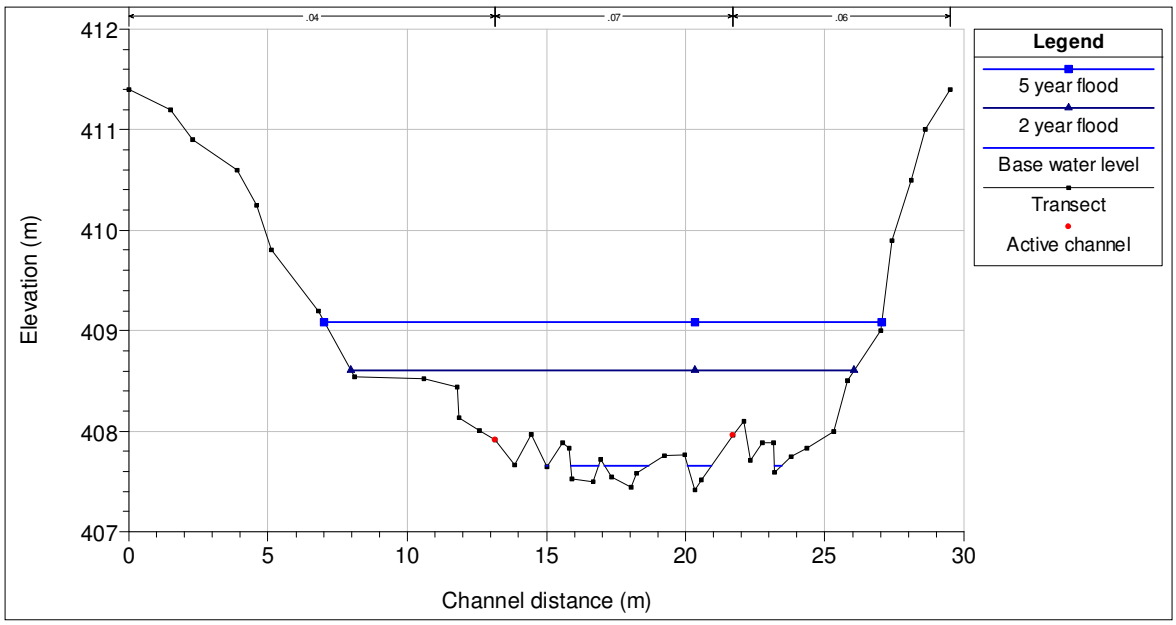


Fig. 2.12 The upstream Macquarie River site (CB). Mature eucalypts are set back from the river channel (upper panel). The lower panel shows the channel profile, with the channel width (m) on the x-axis, and elevation above sea level (m) on the y-axis. The black line is the surveyed transect, with the active channel width indicated by a red dot. The horizontal blue lines indicate the presence of disconnected pools at base flow and the extent of 2 year (in black) and 5 year frequency floods into the riparian zone.

The downstream Macquarie site (IF) is adjacent to the private sheep grazing property, Island Flats (upper panel Fig. 2.13), and has a shallow timber bridge upstream of the study site. Tooms River forms the southern boundary of this property. The topography is generally of low relief (lower panel Fig. 2.13).

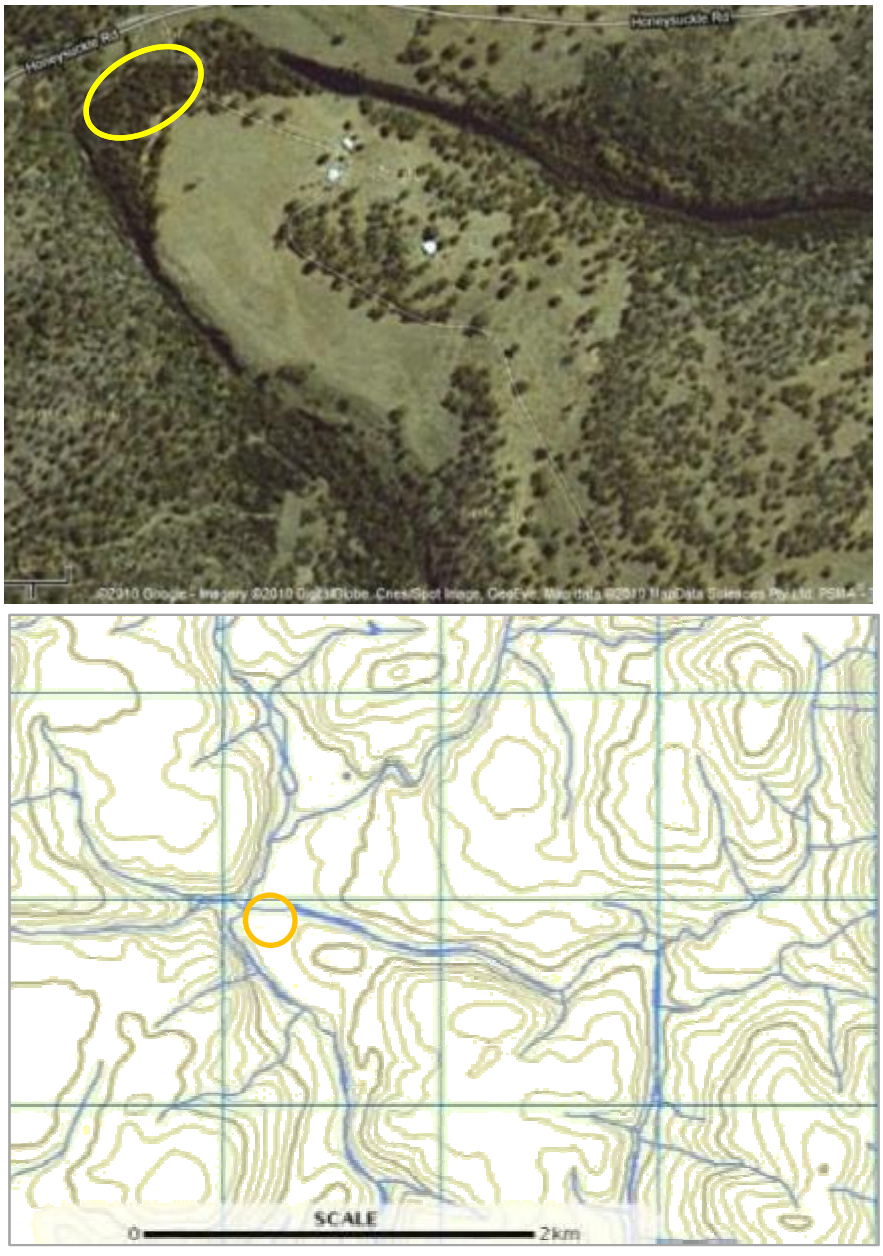


Fig.2.13 Satellite image of the downstream Macquarie site, IF, adjacent to the grazing property Island Flats (upper panel). The study site is in the top left corner of the river, with flow from right to left (Google Maps, 2010). The lower panel is a topographic contour map, with contours at 10 m intervals in grey and the river and minor tributaries in blue. The study site is outlined in yellow (modified from The List (2009)). The thicker blue line is a broadwater pool.

The southern bank is largely natural, with *E.barberi* and *E. viminalis* over a dense riparian band of *Leptospermum* spp. and *A. mucronata* (upper panel, Fig. 2.14), and with young eucalypts, grasses and graminoids on the northern bank. The profile plot (lower panel, Fig. 2.14) illustrates the incised nature of the channel. Floods that occur at an average frequency of 2 years overflow the channel.

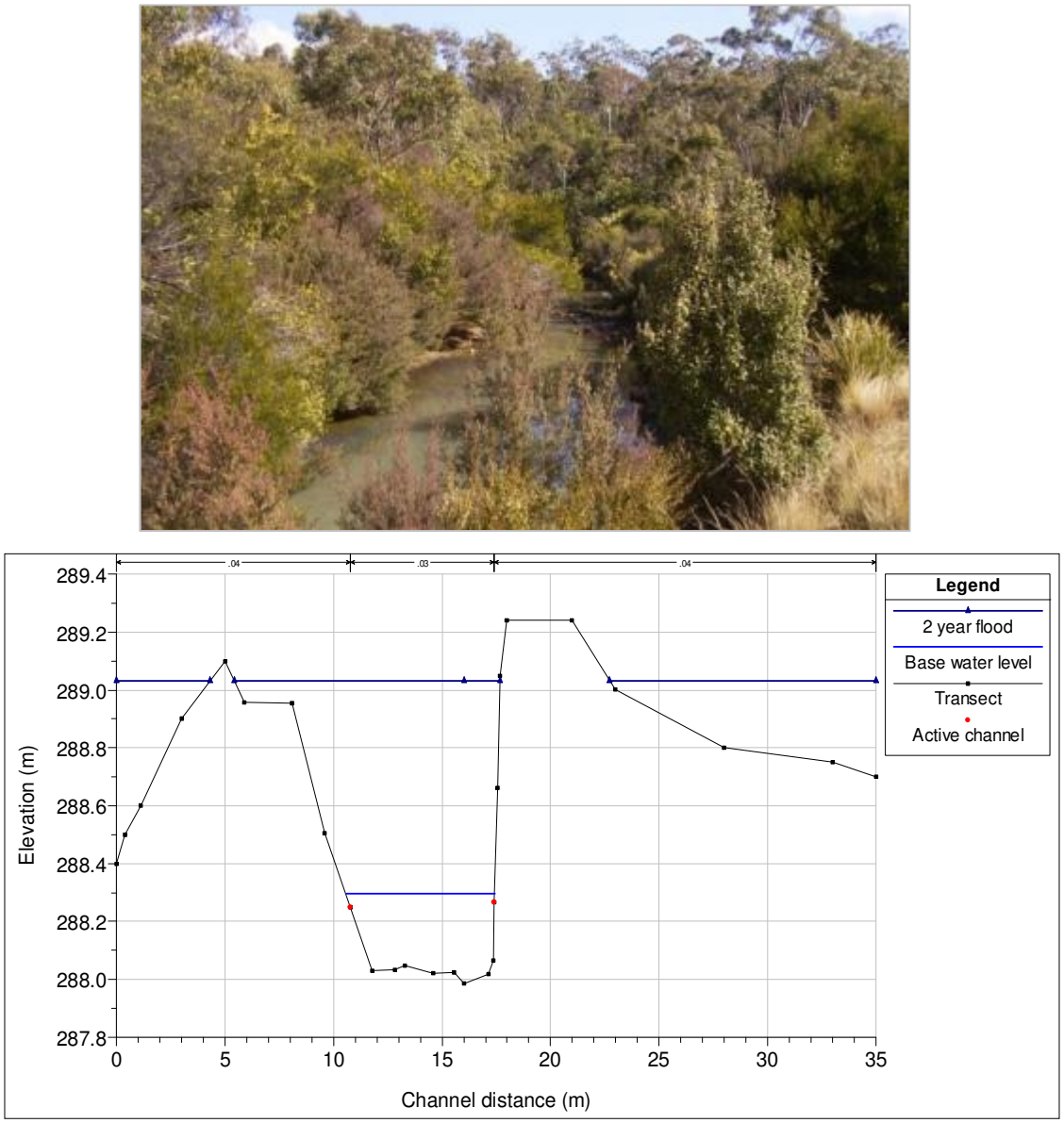


Fig. 2.14 Riparian vegetation (upper panel) and channel profile (lower panel) of the downstream Macquarie site, IF, with the channel width (m) on the x-axis, and elevation above sea level (m) on the y-axis. The black line is the surveyed transect, with the active channel width indicated by a red dot. The horizontal blue line indicates base flow and the extent of 2 year frequency floods (in black) into the secondary channel on the left bank and the riparian zone.

The confined channel at this site is narrower, but deeper, than the channel at the upstream Macquarie site, CB. This conflicts with the expectation that the channel should widen and deepen with the greater discharge as the catchment area increases (Dunne and Leopold 1978), as occurs with the Tooms sites. The narrow channel at the downstream Macquarie site may be a result of the large broadwater upstream of the Island Flats study reach. Broadwaters are deep (up to 30m) pools, restricted to the Macquarie and North Esk Rivers (DPIPWE 2009), although this broadwater is likely to be less than 10 m deep. The upstream pool slows the water flow to the extent that vegetation has established in the stream bed upstream of the study site, which further restricts the effects of high flows. The landscape adjacent to IF is of low relief, so there is limited surface runoff.

2.8.2 Tooms River sites

The upstream Tooms study site (TL) is approximately 1 km downstream of the dam wall, and 400 m downstream of a gauging weir, in a joint water catchment and *Eucalyptus viminalis* reserve (upper panel, Fig. 2.15). The Lake is artificially stocked with introduced brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout and native elvers (*Anguila autralis*) (IFS 2010), which has encouraged establishment of a fishing community beside the lake. The stream channel is constrained, but the river flows into a series of steep gorges downstream of the study site (lower panel, Fig. 2.15).

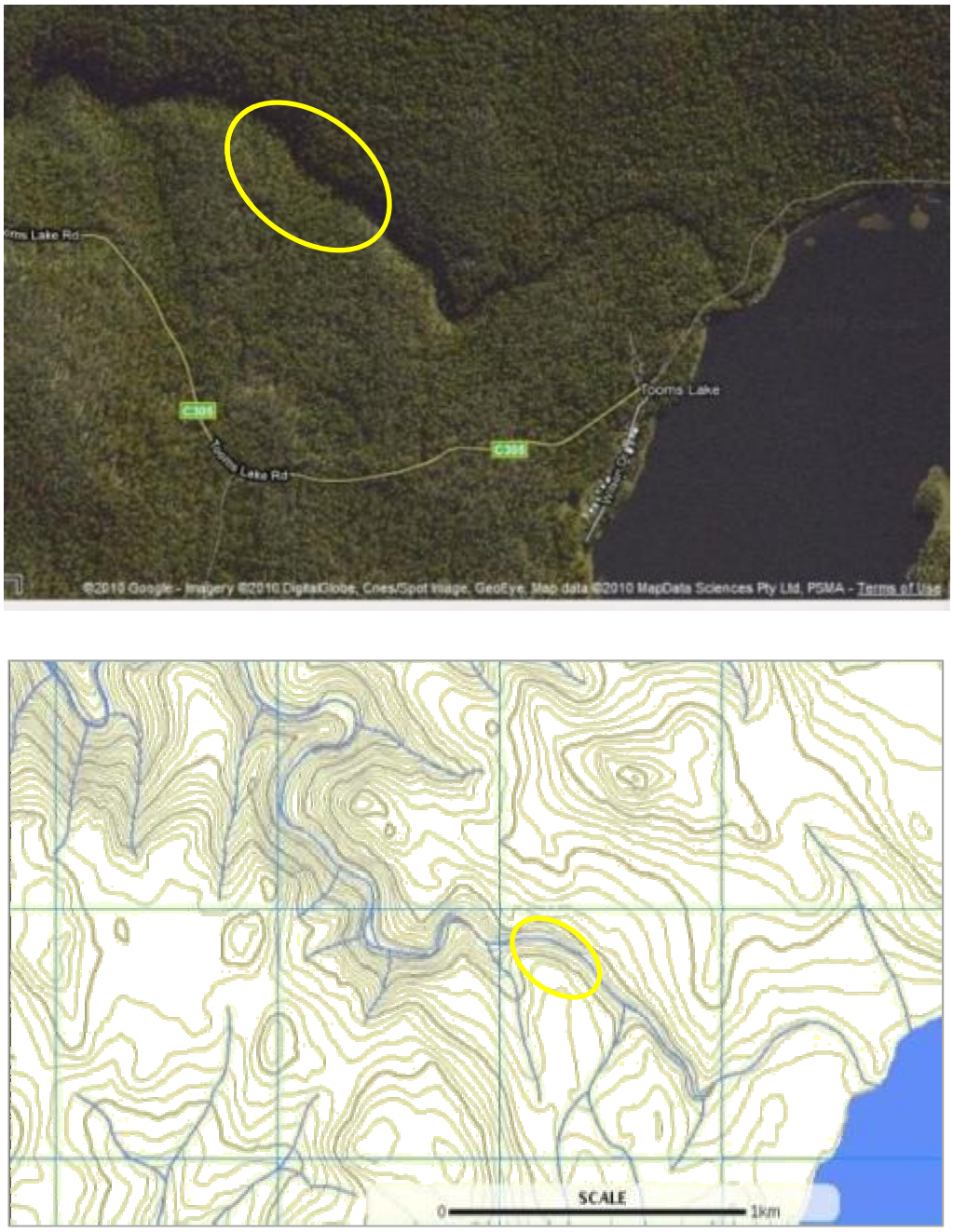


Fig.2.15 Satellite image of the upstream Tooms site, TL, (upper panel) showing the shack community on the lake shore. The dam wall is shown in grey to the north east of the village (Google Maps, 2010). The lower panel is a topographic contour map, with contours at 10 m intervals in grey and the river, lake and minor tributaries in blue. The study site is outlined in yellow (modified from The List (2009)).

The vegetation surrounding the upstream Tooms site, TL, is open dry eucalypt woodland (upper panel, Fig. 2.16). The riparian zone has mature eucalypts close to the river bank, and there is a dense shrub layer, dominated by *A. mucronata, Leptospermum* spp., with a ground layer of bryophytes, ferns and graminoids. The river is heavily shaded by overhanging vegetation (lower panel, Fig.2.16). The channel profile plot (Fig. 2.17) demonstrates the incised channel and the extent of the floodplain on the left bank.

Fig. 2.16 The upper panel shows the open understorey of the dry eucalypt woodland adjacent to the upstream Tooms site, TL. This is distinct from the overhanging riparian vegetation (lower panel), which creates heavy shade at the upstream Tooms River site, TL, where moisture-loving plants are common.

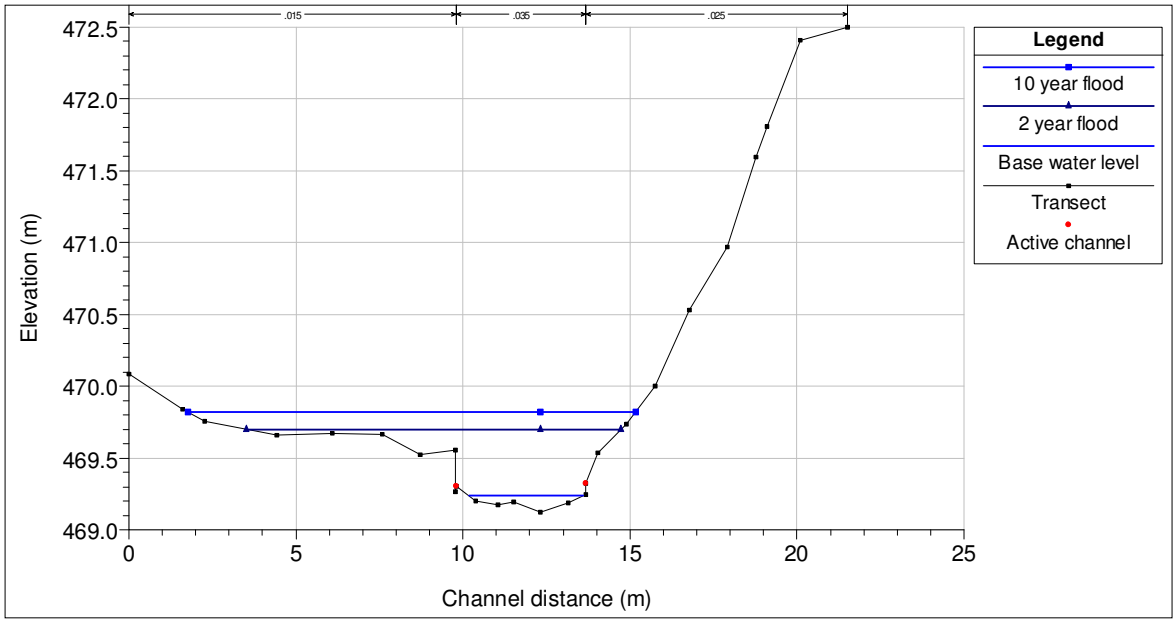


Fig. 2.17 Channel profile of the upstream Tooms site, TL, looking downstream, with the channel width (m) on the x-axis and elevation above sea level (m) on the y-axis. The black line is the surveyed transect, with the active channel width indicated by a red dot. The horizontal blue lines indicate the narrow channel at base flow and the extent of 2 year and 10 year frequency floods onto the left bank floodplain.

The river channel between the two Tooms sites is confined by a steep gorge, opening out to a "bottom" or alluvial plain at the downstream site (BB). This site is accessed through a private grazing property, Blanket Bottom, which has the river as the northern property boundary (upper panel, Fig. 2.18). The topographic map contours show the extent of the alluvial bottom where the river flows from the steep upstream gorges (lower panel, Fig. 2.18).

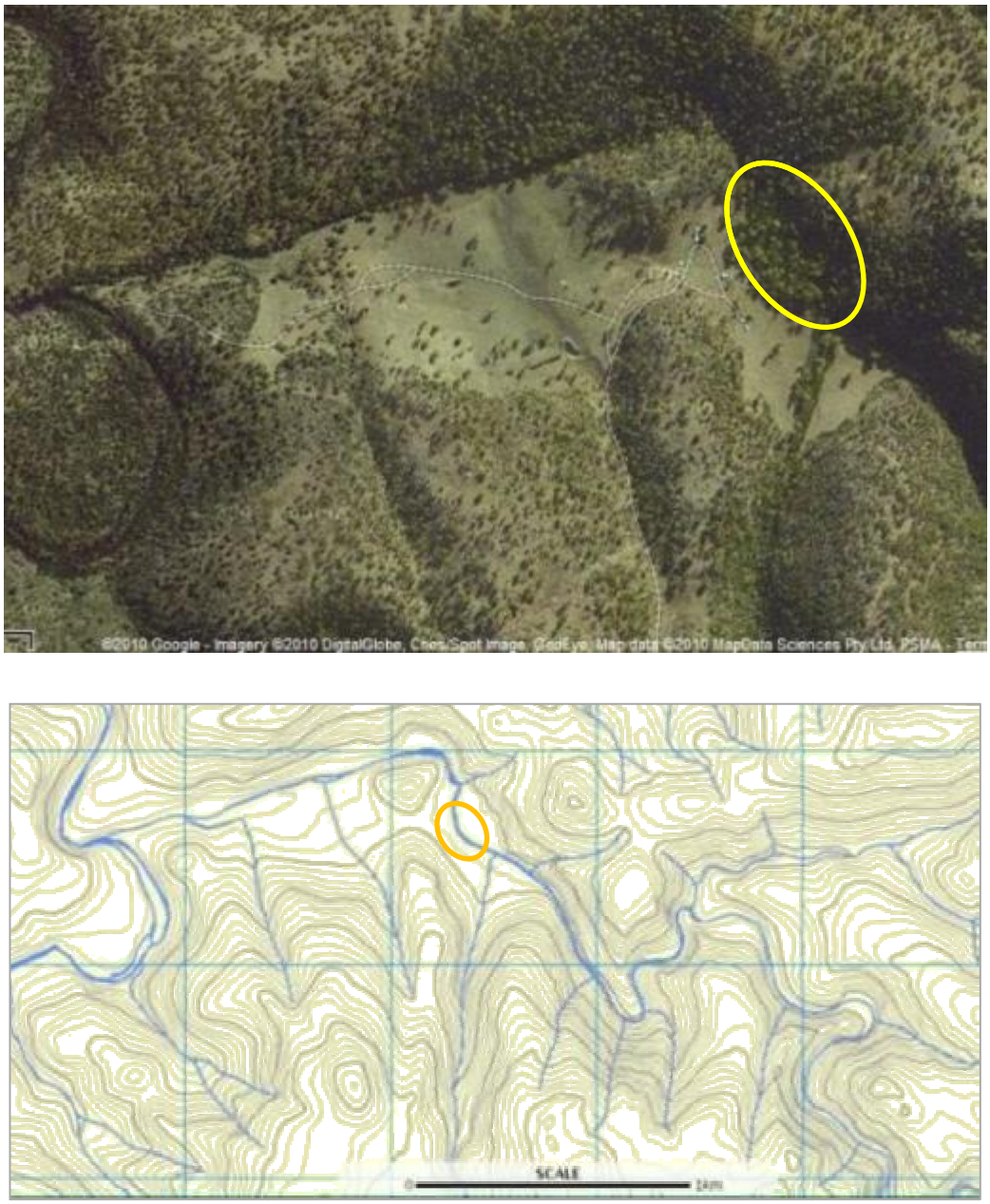


Fig. 2.18 The upper panel is a satellite image of the downstream Tooms site, BB, on the grazing property Blanket Bottom. Tooms River flows right to left, joining the Macquarie River at the centre left. The ephemeral stream shown by a narrow band of trees in the lower right of the photo augments flow after heavy rain (Google Maps, 2010). The lower panel is a topographic contour map, with contours at 10 m intervals in grey and the rivers and minor tributaries in blue. The study site is outlined in yellow (modified from The List (2009)).

Although the surrounding area has been heavily modified by grazing, the riparian zone is essentially unmodified, and is composed of mature eucalypts over a riparian band of mostly *L. lanigerum* and *A. mucronata*, with an understorey of grasses and graminoids (upper panel, Fig. 2.19).

Vegetation extends to the edge of the constrained channel, with no floodplain. The channel profile plot (lower panel, Fig. 2.19) demonstrates the presence of deeper pools at base flow, and historic river terraces on the left bank.

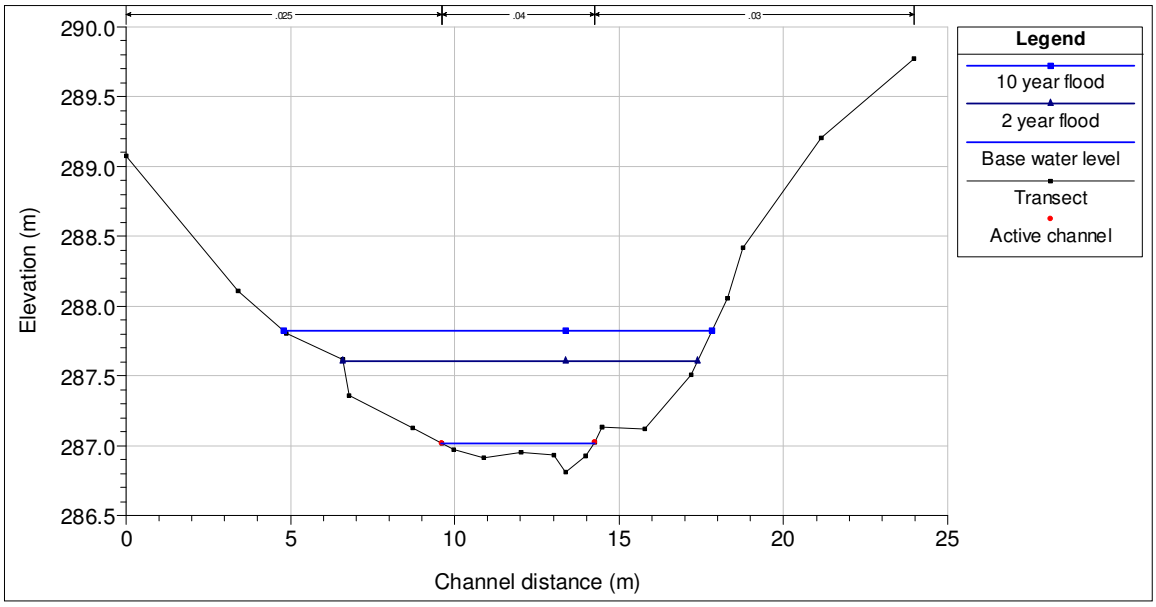


Fig. 2.19 Riparian vegetation at the downstream Macquarie site, BB (upper panel), looking upstream. Mature eucalpts extend to the river edge, with a dense riparian band of *L. lanigerum* and *A. mucronata.* The lower panel shows the channel profile looking downstream. The x-axis shows the channel width (m); the y-axis shows the elevation above sea level (m). The black line is the surveyed transect, with the active channel width indicated by a red dot. The horizontal blue lines indicate the narrow channel at base flow and the extent of 2 year (in black) and 10 year frequency floods into the riparian zone.

While releases from Tooms Lake produce the majority of flow at this site, an ephemeral stream on the eastern property boundary, just upstream of the study reach, provides enough discharge to overturn small cobbles in the stream bed after heavy rain and decreases the influence of the lake discharge on water quality. Several other small streams also enter Tooms River between the two study sites.

2.9 Context of this study

The adjacent regulated Tooms and free-flowing Macquarie rivers were selected on the basis that the similarity in geology and climatic conditions would have originally produced similar ecological conditions in each river. Therefore, any current differences between the rivers could be directly attributed to regulation effects (Braatne *et al.* 2008). However there are unique aspects to every river and potentially to every reach (Naiman *et al.* 2005). The differences between the sites in geomorphology and the current riparian vegetation potentially influence the distribution and accumulation of riparian and benthic litter, the abundance and community structure of biofilms and therefore the availability of allochthonous and autochthonous resources to riverine food webs. The flow regime is likely to be the major factor on all the ecosystem variables. Tooms River has a more stable flow regime than the Macquarie River, with less frequent and smaller floods, and augmented low flows. This is in accord with Petts' (1984) prediction of 1st-order effects on the regulated river system. These changes have produced 2nd-order effects on the geomorphology of Tooms River. The following chapters examine the 2nd-order effects on the riparian vegetation structure, and the 3rd-order effects on benthic resources and macroinvertebrate communities arising from these changes. Individual site characteristics are likely to have a strong influence on these variables (Monk *et al.* 2006).

Chapter 3 Riparian vegetation dynamics in response to flow regulation

3.1 Abstract

Regulation of the flow regime can influence the structure and species composition of the riparian vegetation, with consequences for the abundance and accumulation of plant detritus in the riparian zone, and the movement of plant litter into the water column. Riparian litter fall was monitored with artificial turf mats at upstream and downstream sites on the regulated Tooms River and unregulated Macquarie River. Litter accumulation was highest at the Tooms River sites, where the stable flow regime has allowed encroachment of mature trees to the river's edge. Peak litter fall at the Tooms River sites was seasonally offset to peak litter fall at the Macquarie River sites, but was higher at all sites in 2007, after 2 years of drought. Decomposition of leaf litter and nutrient cycling may also be influenced by regulation of the flow regime. Cellulose decomposition potential was highest on the soil surface at the downstream Macquarie site, but highest in the topsoil at the downstream Tooms site, where soil moisture and organic material content were highest. The lowest levels of soil organic material were at the upstream Tooms site.

3.2 Introduction

The flow regime of a river strongly influences riparian vegetation establishment and growth (Hupp and Osterkamp 1996; Nilsson and Svedmark 2002), by controlling soil moisture gradients and biochemistry, which impact on the physical attributes of the vegetation and plant species composition (Merritt and Poff 2010).

Petts (1984) proposed that the 1st order effects of regulation on the flow regime and geomorphology would produce 2nd order impacts on the riparian vegetation. Flow regulation reduces the frequency and

magnitude of floods and overbank flows (Poff *et al.* 1997; Kondolf and Batalla 2005), leading to channel contraction and changes to riparian vegetation (e.g. Petts 1984; Ward and Stanford 1995a; Nilsson and Berggren 2000; Shafroth *et al.* 2002). For example, the encroachment of riparian vegetation can increase shade (Hupp and Osterkamp 1996; Finlay 2001), while the shallow groundwater downstream of a dam in semi-arid areas has been shown to aid establishment of moisture dependent plant species (Bergkamp *et al.* 2000). The flow regime can also influence the amount of ground water (Poff *et al.* 1997), which can impact on those riverside trees which rely on groundwater rather than direct stream flow (Dawson and Ehleringer 1991; Malanson 1993).

Many studies have attempted to better understand the relationships between the flow regime and riparian vegetation. For example, Anderson and Nelson (2003) measured litter fall from the deciduous species *Populus deltoides* in regulated and unregulated branches of a river system in north-western Colorado. They found more litter and more within–site variability at their unregulated site than at the regulated site. During flood events, deposition of leaf litter was highest at the unregulated site. At both sites, litter fall was reduced under drought conditions. Litter fall on a southern Carolina floodplain was controlled by flood activity, with the lowest litter accumulation in frequently inundated areas (Shure and Gottschalk 1985). The frequency of overbank flooding can also influence the decomposition of fallen leaf litter (Ellis *et al.* 1999; Anderson *et al.* 2003).

The factors influencing litter movement between the riparian zone and the stream channel (Fig. 3.1) are likely to vary at low flows (a) and high flows (b), while imports of litter to the stream channel and exports to the riparian zone depend on the type and structure of the riparian vegetation, and the morphology of the stream channel (Gasith and Resh 1999; Abelho 2001).

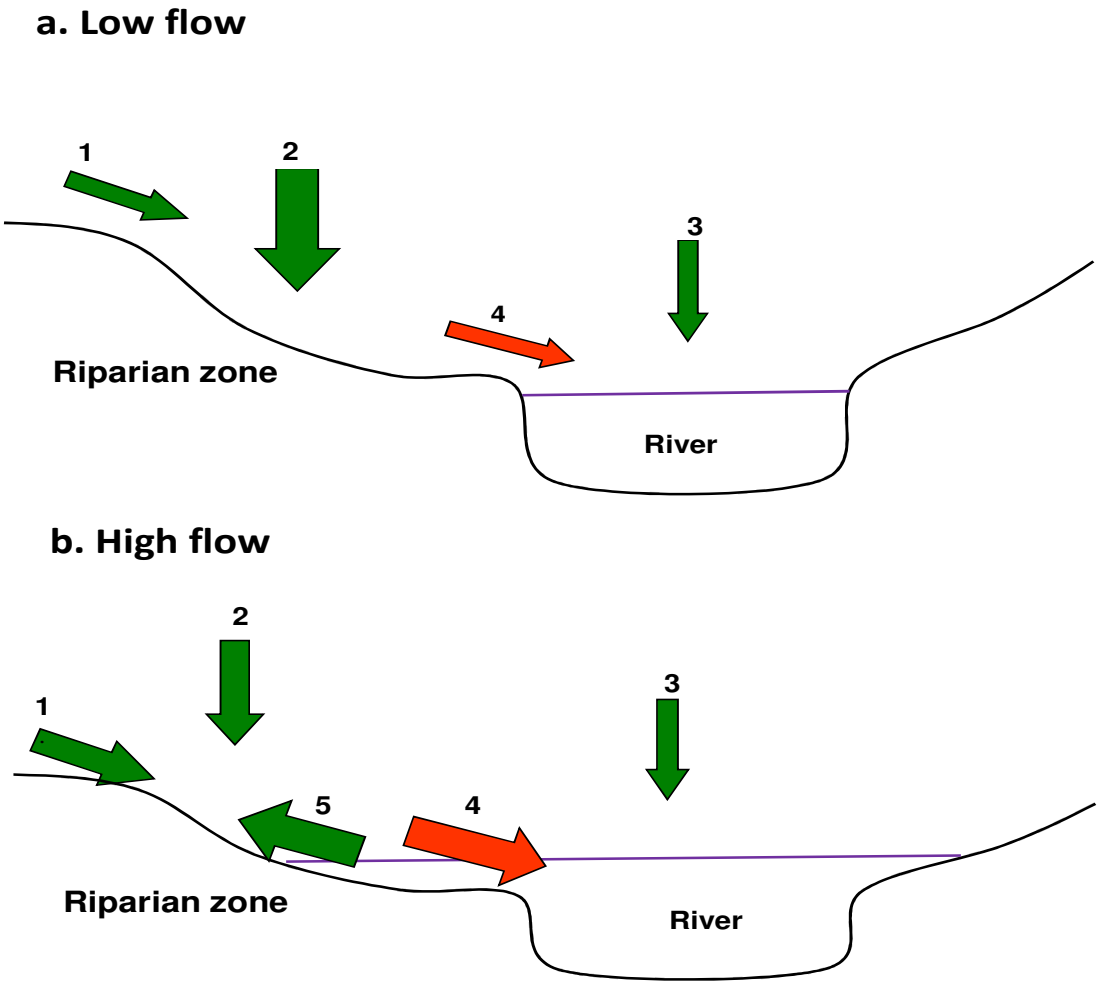


Fig. 3.1 Conceptual model of leaf litter movement between the riparian zone and the stream channel at (a) low and (b) high flows, based on references in Abelho (2001). Litter imports to the riparian zone are shown with green arrows; exports to the stream channel are shown with red arrows. The size of the arrows indicates the strength of the litter movement. Arrows are numbered as follows:

1. **Lateral import** depends on slope, retention structures and groundcover

2. **Vertical impor**t depends on season, vegetation type and weather

3. **Vertical import** depends on season, vegetation type, canopy cover, downstream transport and wind

4. **Lateral export** depends on riparian slope, groundcover, retention structures, rainfall, overland flow, wind, and soil hydrophobicity

5. **Lateral import** depends on discharge, river stage height, retention structures, litter supply in the water column, and transport of litter from upstream

Plant detritus moving from the riparian zone to the stream is a source of nutrients for the riverine ecosystem. This study examines the influence of flow regulation on plant litter accumulation in the riparian zone of the regulated Tooms River, in contrast to litter accumulation at the unregulated Macquarie River. Table 3.1 summarises the major riparian and channel morphology influences on riparian and benthic litter accession and decomposition for the river reaches in this study.

Table 3.1 Potential impacts of riparian structure and in-stream channel features on litter accumulation for each study site. CB and IF are the upstream and downstream Macquarie sites, TL and BB are the upstream and downstream Tooms sites, respectively.

Site	Riparian structure	Impact on riparian litter accession	Channel & in-stream features	Impact on benthic litter accession	Factors affecting litter decomposition	Impact on litter decomposition
CB	Shrubby riparian zone, mature eucalypts set further back from channel	Low proportion of eucalypt litter mass, high proportion of acacia and tea tree litter below shrub layer, summer peak litterfall	Open channel, bedrock, large boulders and riffle – pool sequence. No coarse woody debris, overbank flows	Moderate benthic litter standing stock, wind blown eucalypt leaves, flow driven acacia and tea tree leaves, transport from upstream	Variable soil moisture, controlled by flow regime, high evaporation	Slow decomposition
IF	Shrubby riparian zone, mature eucalypts set further back from channel	Low proportion of eucalypt litter mass, high proportion of acacia and tea tree litter below shrub layer, summer peak litterfall	Narrow, confined, low gradient channel, cobble bed, upstream broadwater, overbank flows. No coarse woody debris	Low benthic litter standing stock Wind blown eucalypt leaves, flow driven acacia and tea tree leaves, low transport from upstream	Variable soil moisture, controlled by flow regime, high evaporation	Slow decomposition
TL	Mature eucalypts beside channel, dense shrub layer over stream, mossy ground cover, abundant CWD	Low proportion of eucalypt litter mass, moderate proportion of acacia and tea tree, summer peak litterfall	Incised, narrow channel, bedrock, boulders and cobbles rare overbank flows. Abundant coarse woody debris, trailing shrubs, upstream dam	High benthic litter standing stock, shrub layer reduces eucalypt leaf input, low litter transport from upstream	Constant soil moisture, continuous flow from dam, low evaporation	Moderate decomposition
BB	Mature eucalypts beside river, dense shrub layer, sedge ground cover	High proportion of eucalypt litter mass, moderate proportion of acacia and tea tree, sedges and grasses in litter, summer peak litterfall	Broader channel, less incised, terraced banks, riffle-pool sequence, boulders and cobbles, input from ephemeral streams after heavy rain, occasional overbank flows. Moderate coarse woody debris, trailing shrubs	High benthic litter standing stock, eucalypt leaves wind blown and direct litterfall, litter transported from upstream, some impact from ephemeral flows	Variable soil moisture, less impact of dam, higher evaporation than at TL	Moderate decomposition

3.3 Methods

3.3.1 Study area riparian vegetation

The structure of the riparian vegetation varies between rivers, and between upstream and downstream sites in this study. Mature eucalypts are set back from the stream channel at the Macquarie River sites (Fig. 3.2), and the riparian zone is dominated by a *Leptospermum* and *Acacia* shrubby understorey. The upstream site (CB) has a boulder and bedrock substrate and a higher gradient than the downstream site (IF), where the substrate is dominated by cobbles. There is no coarse woody debris in the active channel at either site.

Fig. 3.2 a) Upstream Macquarie site, CB b) Downstream Macquarie site, IF. *Acacia* and *Leptospermum* dominate the riparian zone at both sites, with mature eucalypts set back from the stream channel.

Mature eucalypts grow close to the stream channel at both Tooms River sites, although the structure of the riparian vegetation differs between sites, with ramifications for litter accession. At the upstream site (TL), a dense shrub layer overhangs the channel and potentially reduces

eucalypt leaf input, while at the downstream site (BB), the canopy is more open (Figs. 3.3). Coarse woody debris is abundant in the channel at both sites. Both sites have a boulder and cobble substrate, with more bedrock and a higher gradient at the upstream site.

Fig.3.3 a) Upstream Tooms site, TL b) Downstream Tooms site, BB *Acacia* and *Leptospermum* completely shade the upstream site, while the vegetation canopy is more open at the downstream site. Boulders are common at both sites.

The understorey of the upstream site is dominated by mosses and ferns near the channel, with abundant woody debris (upper panel, Fig. 3.4). Sedges and grasses are found where the canopy has been opened by fallen trees and at the outer edge of the riparian zone. By contrast, the downstream site, BB, is relatively open. Here, sedges and grasses dominate the understorey, although there is still abundant woody debris (lower panel Fig. 3.4).

Fig. 3.4 Mosses and rotting woody debris dominate the heavily shaded understorey of the upstream Tooms site, TL (upper panel). The downstream Tooms site, BB, has steeper banks than the upstream site (lower panel), with the understorey dominated by sedges and grasses.

My initial hypothesis, based on the findings of Nilsson and Svedmark (2002) and others, was that the more variable flow regime in the Macquarie River would lead to greater variability in the accumulation of litter in the riparian zone than at the Tooms river sites. However, there were obvious differences between the riparian vegetation and channel

structures of the rivers and the sites chosen for this study. Riparian litterfall was measured at each site to test whether these differences impacted on litter dynamics, with the expectation that the denser canopy at the Tooms River sites would lead to greater litter accumulation. It was considered likely that more constant flow regime at the regulated sites would increase soil moisture levels, and hence accelerate litter decomposition rates, leading to higher soil organic material content, so decomposition on the soil surface and in the upper soil layer was assayed with cellulose strip decomposition. The prevailing drought was expected to have a similar impact on the timing and accumulation of the allochthonous resources of each river.

3.3.2 Riparian litter fall

Artificial turf mats were used to continuously monitor litterfall over 2 years from January 2006 to February 2008. Turf mats have been successfully used in many floodplain sediment studies (e.g. Asselman and Middelkoop 1995; Middelkoop and Asselman 1998; Steiger *et al.* 2003). They were considered ideal to measure litterfall in the current study because the vegetation was too dense to allow for the vertically suspended litter traps that are used in the majority of litter fall studies (e.g. Campbell *et al.* 1992; Cillero *et al.* 1999; Oelbermann and Gordon 2000). This technique also captured more of the small leaves that were typical of the riparian zone at these sites. The mats provided a removable substrate which simulated the natural ground surface and accumulated both vertically and laterally deposited litter.

3.3.2.1 Pilot study

A pilot study was conducted at two sites (BB on the Tooms River, and IF on the Macquarie River) during summer peak litterfall, to determine whether there was any difference in the weekly rate of accumulation of organic matter between a 6-week and 12-week period of exposure. At each site, nine pairs of 250 mm x 250 mm Astroturf® synthetic grass

mats, with 18 mm long leaf blades, were pinned to the ground with one 150 mm steel nail at each corner (Fig. 3.5). One randomly selected mat from each pair was replaced with a new mat after 6 weeks and both remaining mats were recovered after a further 6 weeks. All mats were processed as for the long term study as detailed below (3.3.1.3)

Fig.3.5 Paired mats in position for 6 weeks: 12 weeks replacement pilot study.

Biomass of organic material (OM) was expressed as grams dry weight accumulated per 30 days, and these data were log-transformed to meet the assumptions of ANOVA. There was no difference in the biomass accumulated per 30 d between the two 6-week periods (mixed-model ANOVA using site as a random block effect ($F_{(17,17)} = 0.738$, $p = 0.73$), nor was there any difference between mats exposed for 6 or 12 weeks ($F_{(1,51)} = 0.085$, $p = 0.77$). Therefore there was no evidence that extending exposure times to 12 weeks impacted on the rate of OM accumulation on these mats, which allowed for flexible exposure times of between 6 and 12 weeks as logistic and climatic conditions allowed.

3.3.2.2 Riparian litter fall study

For the long term trial, nineteen mats were used at each of the four study sites. Before placement of each mat, the existing standing stock of leaf litter was collected from the soil surface within a defined 250 x 250 mm area, down to the firm ground surface. Nine of the mats were deployed adjacent to the water line at each site, each centred on a 4 mm x 250 mm mild steel erosion pin. A further 5 mats were deployed at each of 1 m and 2 m from the water edge (Fig. 3.6). Distance from the water's edge was limited by the dense riparian vegetation of the Macquarie River sites, and maintained across all sites for consistency. The different channel form of the regulated and unregulated sites prevented standardisation of the vertical distance above the waterline between sites, but the variation between sites for each mat distance was less than 200 mm. Owing to the drought, there was no measureable difference in soil surface levels on the erosion pins throughout the study period.

After six weeks, the mats, with all contents, were transferred to individual ziplock bags, and replaced with a new mat in the same position. Mats were replaced again after a further 6 weeks. Replacement was increased to 3 month intervals when litter fall decreased in winter and maintained at this interval for the remainder of the project, except for the last round, when collection was delayed for an additional 6 weeks. At site CB, a rotten tree fell across one of the mats in summer 2007-08, resulting in a large amount of wood fragments. For data analysis, the wood component was excluded from the litter for this mat, since this was several orders of magnitude greater than the wood collected by any other mat in this study and could be clearly discerned from normal wood deposition.

Five mats were also deployed in the shallow edge zone of the Tooms River channel from March 2006, where *Leptospermum* roots intruded into the

wetted channel at both sites (Fig. 3.6). This was based on the observation by Speaker *et al.* (1984) that plant roots extending into the stream channel could trap organic detritus moving in the water column. Because the 'wet' mats were only used at the Tooms river sites, the data were analysed separately from the main mat data.

Fig. 3.6 Astroturf® mat placement at TL. The upper mat is close to the water line (edge mat), centred on an erosion pin. The lower mat is a 'wet' mat in the shallow root zone at low flow.

3.3.2.3 Laboratory processing

In the laboratory, each mat and its contents were transferred to a clean aluminium tray, dried to constant mass (48 h, 50 ^{o}C), then weighed to the nearest 0.01 g. The leaf litter was removed by beating the mat in a standardised way (4 hard beats with a wooden rod) after combing with a coarse-toothed steel comb. Woody material was separated into wood fragments > 5 mm diameter; twigs < 5 mm diameter; and bark and woody seed capsules, identified to genus. All woody components were weighed to 0.01 g on an electronic balance. Leaf material was spread in a white plastic sorting tray and sorted to the species level where possible,

otherwise to genus. The abundance of each species was visually assessed using the Braun-Blanquet (1932) scale of 0, 1 = 0-10%, 2 = 10-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-100%. Unidentified organic fragments were classed as 'other'. Litter from the initial standing stock was similarly treated, with the fine fraction (< 500 µm) ashed (4 h, 550 ^{o}C) to determine the inorganic content.

The percentage canopy cover above each group of mats was calculated from vertical photos taken 500 mm above the ground surface, with a Powershot G9 digital camera (Canon Inc., Japan) fitted with a 0.42 x fisheye lens, which produced a 178^{o} field of view. The proportion of canopy closure was determined with particle analysis of binary images with the program ImageJ (Rasband 2010).

3.3.2.4 Data analysis

Data were analysed using R version 2.11.0 (R Development Core Team 2010). Linear mixed models tested for differences between sites. A model was fitted for each dependent variable that included site (4-level factor) and its interactions with the periodic terms. Periodic regression was used to describe any trends over the annual cycle for riparian and benthic root zone litter mass, since cyclical, seasonal changes are usually over a year with these variables. Individual mats were treated as the random effect and total leaf mass and total litter mass (expressed as mass per square metre, standardised to 30 day periods) and date were treated as the fixed effects. Sample dates were expressed as the proportion of a calendar year, t. The dependent variable, y, was regressed on the sine and cosine of the re-expressed sample date, t, converted to radians:

$$y = a_0 + a_1 \cos(2\pi t) + a_2 \sin(2\pi t)$$

The estimated parameters from this regression equation were rearranged to derive estimates of the overall mean (or mesor) of the cycle, its

amplitude (i.e. the maximum or minimum value as measured from the mean) and the phase angle, θ, which is the point in time of the maximum of the cycle. Computational details are given in Batschelet (1981).

A model was initially fitted for each dependent variable that included site (4-level factor) and its interactions with the periodic terms, but there was always at least one significant interaction. Therefore separate regressions were conducted for each site, with parameter estimates and standard errors computed and tabulated for each significant term.

Because there was only a single collection of the litter standing stock, single factor ANOVA of log transformed data tested for significant differences between rivers and sites in the total litter mass. Tukeys HSD (Honest Significant Difference) test indicated the sites which contributed to differences where a significant effect was detected. The initial standing stock of litter and the components of the mat litter were also analysed in PRIMER 6.1.9 (PRIMER-E Limited 2007), with analyses based on a Bray-Curtis dissimilarity matrix. Woody and leafy components of litter were analysed separately, because different methods were used to assess their abundances. ANOSIM (analysis of similarity) calculated the significance level of differences between variables. The SIMPER (similarity in percentages) routine examined the contribution of each variable to the differences between the sites and rivers.

3.3.3 Terrestrial cellulose decomposition

3.3.3.1 Field protocol

In the 2007-2008 summer, cotton strip assays were used to test the rate of cellulose decomposition in the riparian zone, as a surrogate for leaf decomposition (Boulton and Quinn 2000). Although Tiegs *et al.* (2007) showed that cellulose strip decomposition did not always correlate strongly with leaf decomposition, they suggested that it was appropriate

for comparing decomposition between sites, but may be more indicative of microbial activity than invertebrate feeding activity. This technique also avoided a number of logistic issues relating to the number of leaf species that would need to be quantified, and the difficulty of testing the small leaves of the prevalent riparian species.

All trials used 35 mm x 60 mm strips of unbleached cretonne EMPA 222 test fabric (EMPA Testmaterials: St Galen). Decomposition on the soil surface was tested with single cotton strips, each stapled to a 40mm x 120mm x 7mm mesh strip of lightweight PVC gutter mesh (Buy Right™, Mitre 10 Australia Ltd). The free end of each strip was nailed to the ground beside a turf mat (n = 9) at each site, with the cotton in contact with the ground surface (Fig. 3.7). Handling effects were assessed by nailing 3 control strips in place at each site, then immediately removing each strip and sealing it in an individual ziplock bag.

Fig.3.7 Surface cotton strips (inset) were held against the ground surface beside the sediment mats with the steel nail securing the mat.

Decomposition in the humic soil layer was tested by attaching paired cotton strips to each side of a 40mm x 70mm strip of gutter mesh with steel staples (Figure 3.8). These were deployed beside the turf mats (n

= 9) in the riparian zone at each site. Each paired strip (hereafter 'panel') was inserted lengthwise into a 60 mm deep slot in the soil, and the soil was compressed against the strip with a stainless steel trowel. Three control panels were buried at each site and then retrieved immediately to assess handling effects.

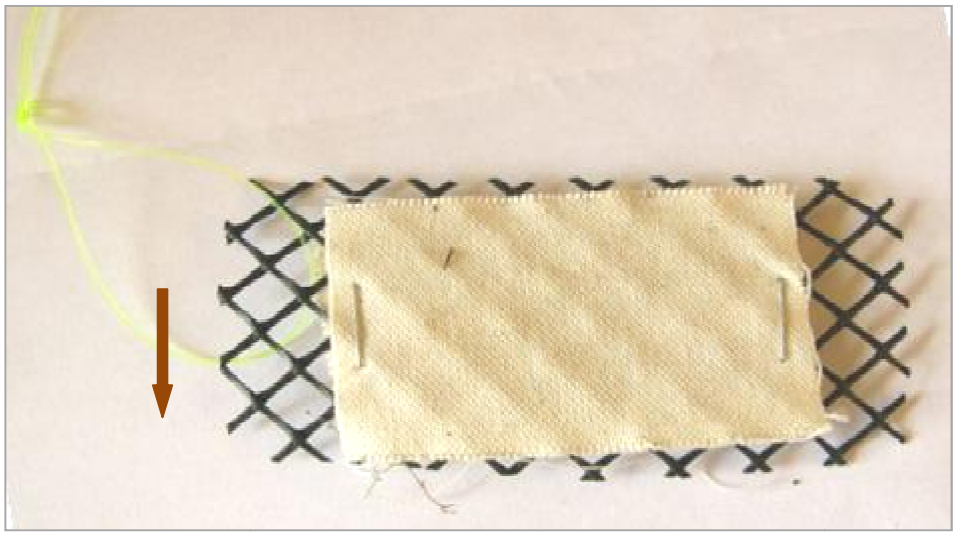


Fig.3.8 Paired cotton strips were attached to either side of mesh panels and inserted vertically into the topsoil.

3.3.3.2 Laboratory protocol

At the upstream Macquarie site, CB, one surface strip and one buried panel were lost to overbank flow on about day 13. All the remaining strips were retrieved after 40 days and air-dried at room temperature. Tensile strength was measured with a tensiometer (University of Tasmania, Australia) incorporating a Salter Electro Samson scale (Kent, UK).

The tensile strength (kg) of the cotton was determined by fastening each strip into the 40 mm jaws of the tensiometer, and recorded as the breaking point of the resultant 35 x 40 mm strip. Cotton tensile strength loss (CTSL) was calculated by subtracting the strength of exposed strips from the strength of controls. Because the paired buried strips were pseudo-replicated, the mean CTSL of the 2 strips was

calculated. Data analysis used the *nlme* package (Pinheiro *et al.* 2009) in R 2.11.0 (R Development Core Team 2010). The influence of soil physicochemical variables on cotton strip strength loss was tested using Pearsons correlation coefficient.

3.3.4 Soil characteristics

Six soil samples (approximately 100 g) were randomly collected at each site from the top 50 mm of soil (A horizon) at the time of cotton strip placement in summer 2007-08, and sealed in individual ziplock bags. In the laboratory, the soil was sub-sampled for pH and measurements of organic content. The pH was measured with a soil pH test kit (Manutec Pty Ltd, Cavan, SA). Water content of the soil samples was calculated by subtracting dry mass (48 h, 30 ^{o}C) from the initial wet mass of the sub-sample. Inorganic content (AFDM) was calculated by subtracting ash weight (4 h, 550 ^{o}C), which was corrected for dehydration of clay particles, from dry weight (Gordon *et al.* 2004). Organic content was expressed as a percentage of the original dry mass of the sub-sample.

3.4 Results

3.4.1 Initial standing stock of leaf litter

The initial standing stock of litter was patchily distributed at all sites. The total litter mass was highest at the upstream Macquarie site, CB and lowest at IF, the downstream Macquarie site. Whereas analysis of variance did not detect a significant difference between the rivers in total litter mass per square metre ($F_{(1, 90)} = 0.289$, $p = 0.592$), multivariate analyses of the total data set with the ANOSIM procedure detected a marginally significant difference between the rivers (Global R: 0.032, $p = 0.05$). However, univariate ANOVA indicated a highly significant difference in total litter mass between sites ($F_{(3, 88)} = 6.206$, $p = 0.0007$). Tukeys test showed that this was generated by significant differences between CB and TL ($p = 0.0073$), and CB and IF ($p = 0.002$) while there was a marginally significant difference between BB and IF ($p = 0.058$).

Pairwise tests with ANOSIM, in contrast, showed that while all sites were significantly different to each other, litter standing stock at CB was closer to the two Tooms sites, TL and BB than to the other Macquarie site, IF. There was very high within-site variability in both total litter and woody litter (Table 3.2). Leaf mass was lowest at IF and TL, and woody mass formed a greater percentage of the total litter at those sites than at CB and BB. While total litter mass increased with distance from the water edge at all sites (Table 3.3), separate analyses showed that this was only significant at the upstream Macquarie site, CB ($F_{(2, 22)} = 5.223$, $p = 0.01$) and at the lower Tooms site, BB ($F_{(2, 22)} = 6.044$, $p = 0.008$).

Table 3.2 Mean total mass (g. m^2) and mean woody mass (g. m^2) of initial litter standing stock, ± 1 standard deviation

River	Site	Mean total mass ($g.m^2$)	Mean woody mass ($g.m^2$)	Woody: total mass %
Macquarie	CB	1171.2 ± 960.5	219.4 ± 339.8	18.73
Macquarie	IF	339.8 ± 329.0	138.9 ± 236.5	40.87
Tooms	TL	492.5 ± 562.2	151.2 ± 226.9	30.70
Tooms	BB	661.3 ± 527.7	1130.6 ± 137.9	19.74

Table 3.3 Mean mass ($g.m^{-1}$) of initial litter standing stock with distance (zero, one and two metres) from the water's edge, ± 1 standard deviation

River	Site	0 m ($g.m^{-1}$)	1 m ($g.m^{-1}$)	2 m ($g.m^{-1}$)
Macquarie	CB	549.2 ± 620.4	1237.4 ± 862.4	1904.7 ± 867.5
Macquarie	IF	239.7 ± 23.2	345.6 ± 331.1	434.0 ± 478.1
Tooms	TL	174.2 ± 108.9	548.0 ± 762.2	846.1 ± 429.0
Tooms	BB	258.9 ± 105.4	791.6 ± 484.3	1011.5 ± 570.5

SIMPER analysis of the leafy components showed that the proportions of eucalypt leaves and sedge blades distinguished BB from all other sites

(Appendix 1). Eucalypt leaves contributed 27.93% to the similarity of the regulated sites, with *Acacia* phyllodes contributing a further 25.27%. *Acacia* phyllodes (31.51%) and 'other' were more important at the unregulated sites CB and IF, with eucalypts only contributing 14.61% to the similarity between the sites. The abundance of *Allocasuarina* phyllodes and *Juncus* blades separated the downstream Macquarie site IF from all other sites. The upstream Macquarie site, CB, and the downstream Tooms site, BB, were 70.51% similar, the closest of all the sites.

Pairwise ANOSIM indicated that the woody components of standing litter stock were significantly different ($p < 0.05$) at each site. SIMPER analysis showed that twigs were the main woody component at all sites. There were more eucalypt capsules at the Tooms River sites than the Macquarie sites. When the 4 sites were compared, bark and twigs were more abundant at the upstream Macquarie site, CB than the other 3 sites (Fig. 3.9). Bark was more abundant at TL and CB than at the other sites. There were more *Acacia* pods at the downstream Macquarie site, IF than the other sites, while they were absent from TL.

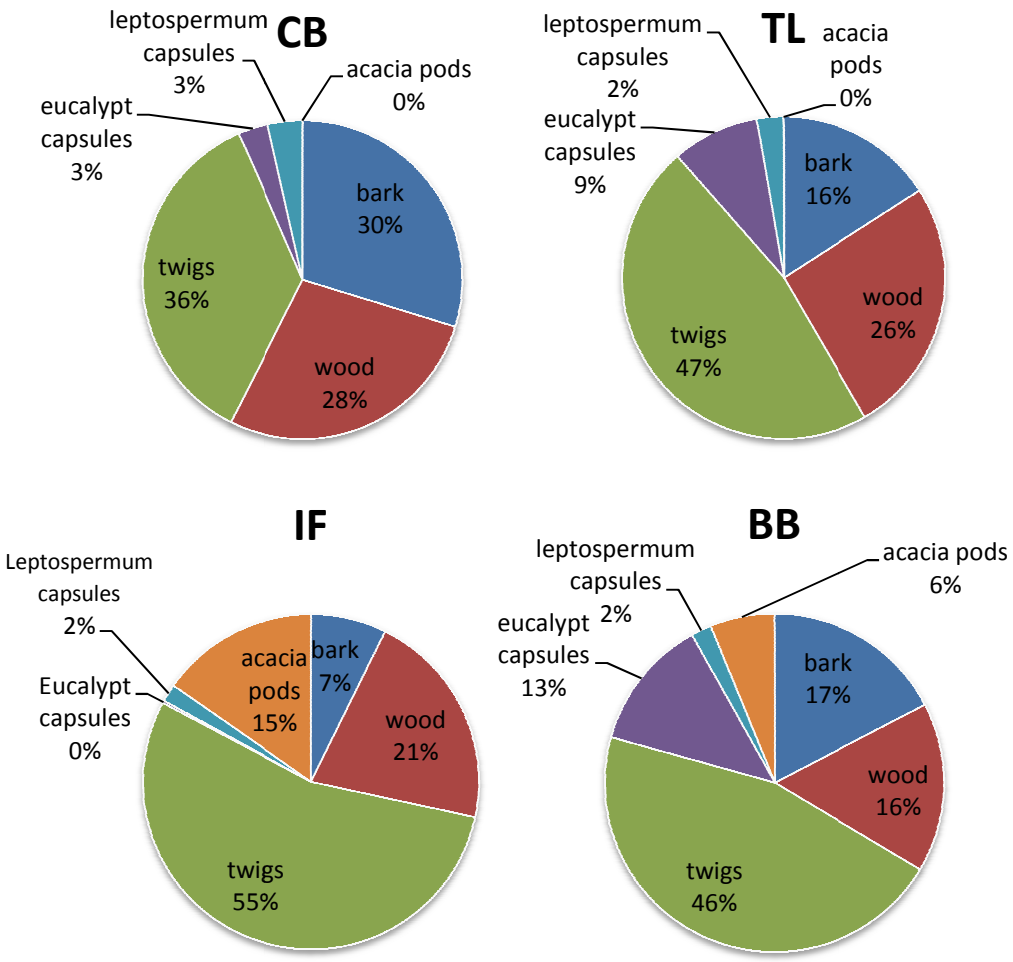


Fig. 3.9 Woody components of riparian litter standing stock, with the upstream sites on each river (CB and TL) shown in the top panel and the downstream sites (IF and BB) shown in the lower panel. The size of the segments in each chart shows the percentage contribution of that component to the total amount of accumulated woody litter.

3.4.2 Riparian litter fall

There was a highly significant seasonality of litter fall at all sites, but the greatest effect was at the Tooms River sites (Table 3.4). The abundance of leaves and fruit in the litter contributed more to differences between the rivers and sites than wood, bark or twig production.

Table 3.4 Significance of seasonal variation in riparian litter fall at each site

Site	$F_{(1.152)}$	p
TL	59.6	$p < 0.001$
BB	16.4	$p < 0.001$
CB	13.4	$p < 0.001$
IF	12.2	$p < 0.001$

Litterfall was similar at the Tooms River sites, but higher at the downstream Macquarie site, IF, than at the upstream site, CB. Seasonal differences in litter fall were greater at the regulated sites, with much greater amplitude. Peak litterfall was in mid-March at the regulated sites, but in late January to early February at the unregulated sites. Peak litter fall was 44 days earlier at CB than at the Tooms sites (Fig.3.10, Table 3.5).

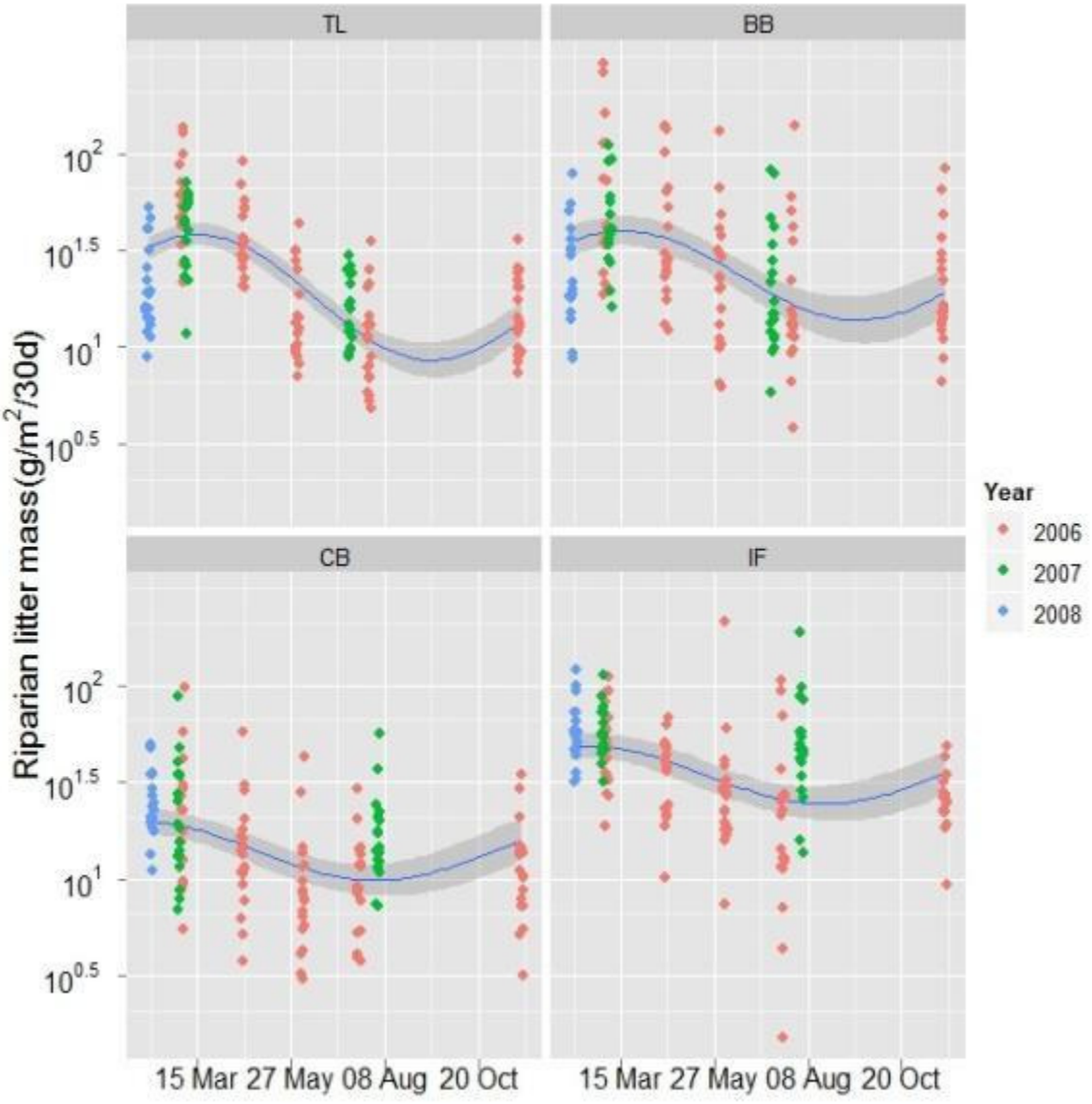


Fig. 3.10 Log_{10} riparian leaf mass accumulation ($g.m^2$ per 30 days) for all study sites, commencing January 2006. TL and BB represent the upstream and downstream sites on Tooms River, respectively; CB and IF are the upstream and downstream sites on the Macquarie River. Dots represent individual sediment mats, with the year of collection indicated by the colours in the legend. The blue line shows the periodic regression trend over the 2 years, with 95% confidence intervals in grey.

Table 3.5 Parameter estimates from the periodic regressions of riparian litter mass, with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the $\log_{10}$-tranformed scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the $\log_{10}$-transformed scale, and the "Date" is the date of this maximum value. (The date values have been back-transformed from the phase angle values, θ, which are not shown here).

Site	Mean	Arithmetic mean	Amplitude	Date
TL	1.26 (1.13, 1.38)	18.1 (13.6, 24.1)	0.325 (0.118, 0.625)	Mar 15 (Mar 04, May 27)
BB	1.37 (1.29, 1.45)	23.5 (19.4, 28.3)	0.230 (0.090, 0.424)	Mar 16 (Mar 05, May 18)
CB	1.14 (1.03, 1.25)	13.9 (10.8, 17.9)	0.152 (0.148, 0.425)	Jan 30 (Sep 12, Feb 13)
IF	1.54 (1.4, 1.67)	34.4 (25.3, 46.7)	0.149 (0.191, 0.489)	Feb 18 (Aug 23, Feb 20)

Mean litter fall was consistently higher at the Tooms River sites, but all sites had higher litter fall in 2007 than 2006. The highest cumulative total litter was at the downstream Macquarie site, IF, at all distances from the water's edge. There were highly significant differences between the regulated (Tooms) and unregulated (Macquarie) Rivers (Global R: 0.234, $p < 0.001$), but differences in total litter accumulation between sites within rivers were not significant. There was no *Allocasuarina* foliage and low *Acacia* pod volume at the regulated sites, where bark and eucalypt leaves and capsules were more abundant. Within the Tooms River sites, there were more *Acacia* pods, sedge, *Juncus*, and *Pomaderris* at the downstream site, BB, while there were higher levels of *Banksia* leaves at TL. Differences between the Macquarie River sites were in higher levels of *Acacia* pods, sedge, *Juncus*, and *Allocasuarina* foliage at the downstream site, IF, than at CB. All sites were significantly different

to each other in all rounds ($p < 0.05$), except between the two Tooms sites, BB and TL, in autumn 2006 (round 3) (Global R: 0.072, $p = 0.041$).

There were differences in the seasonal abundance of individual leaf species (Appendix 2). *Acacia mucronata* leaf abundance was highest at CB in most seasons, and was generally lowest at TL. *Leptospermum* leaves were most abundant at IF, followed by TL. Most sites had peak *Leptospermum* litter abundance in summer, with litter abundance peaking at CB after the spring 2007 spate. Eucalypt leaf abundance was higher at all sites in summer 2007-08 than in summer 2006-07. Lowest mean eucalypt leaf fall was at CB, while highest eucalypt leaf fall was at TL in most seasons.

Fruit abundance also varied between sites. Eucalypts produced more capsules at the regulated river sites, with a strong peak in summer 2007- 08. Eucalypt capsule mass was lowest at CB, but increased over time at the downstream Macquarie site, IF. Both *Acacia* and *Leptospermum* mean fruit mass were highest at IF. They were less abundant at all sites with high flows.

The distance of mats from the water edge had a significant effect on litter mass at the two downstream sites, BB and IF. The lowest litter mass occurred at 0 m, and increased with distance from the waters' edge. There was no significant difference in litter mass with distance from the water at the upstream Tooms site, TL. In contrast, litter mass at the upstream Macquarie site, CB, was lower at 1m than the other distances (Fig. 3.11).

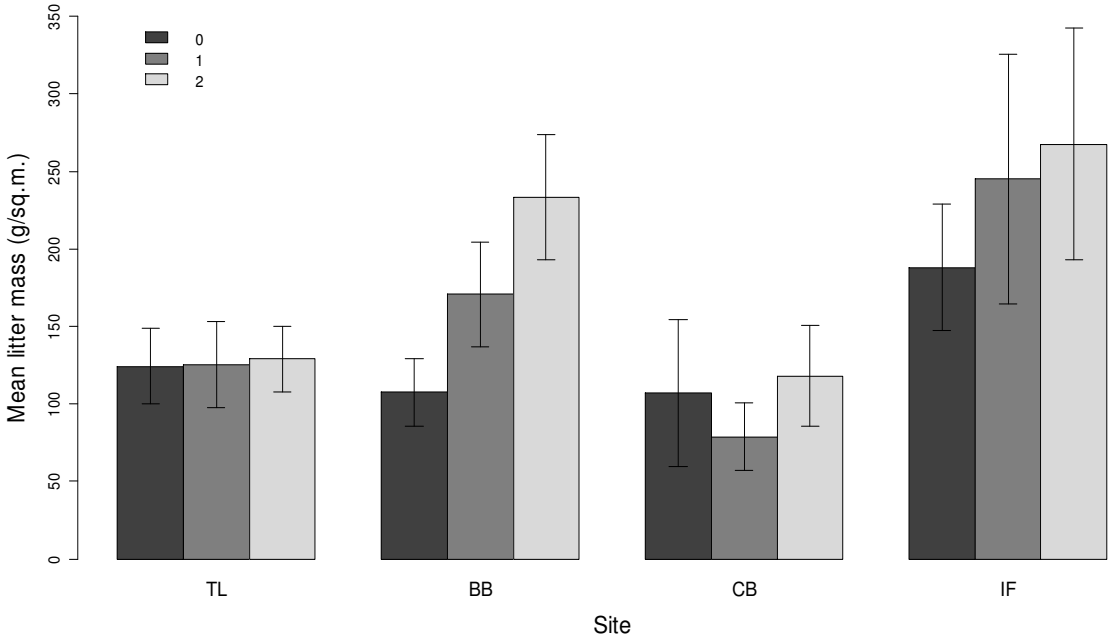


Fig. 3.11 Mean litter mass accumulation per site at 0, 1 and 2 m distance from the waters edge. The height of the bars indicates mean litter mass ($g.m^{-2}$) ± 95% confidence intervals. TL and BB are the upstream and downstream Tooms sites; CB and IF are the upstream and downstream Macquarie sites, respectively.

The accumulation of leaf litter on the 'wet' mats in the root zone of the Tooms River channel (standardised to 30 day periods) was significantly higher ($F_{1, 58}$ = 37.039, p < 0.001), but more variable at BB than at TL. The wet mats were not deployed until round 2, and only at the Tooms River sites. There was significant seasonal variation in litter mass at the upstream site, TL ($F_{(1, 35)}$ = 11.10, p = 0.0002) and at the downstream site, BB ($F_{(1, 35)}$ = 6.79, p = 0.0035). Peak litter abundance was in summer at both sites (Fig. 3.12, Table 3.6).

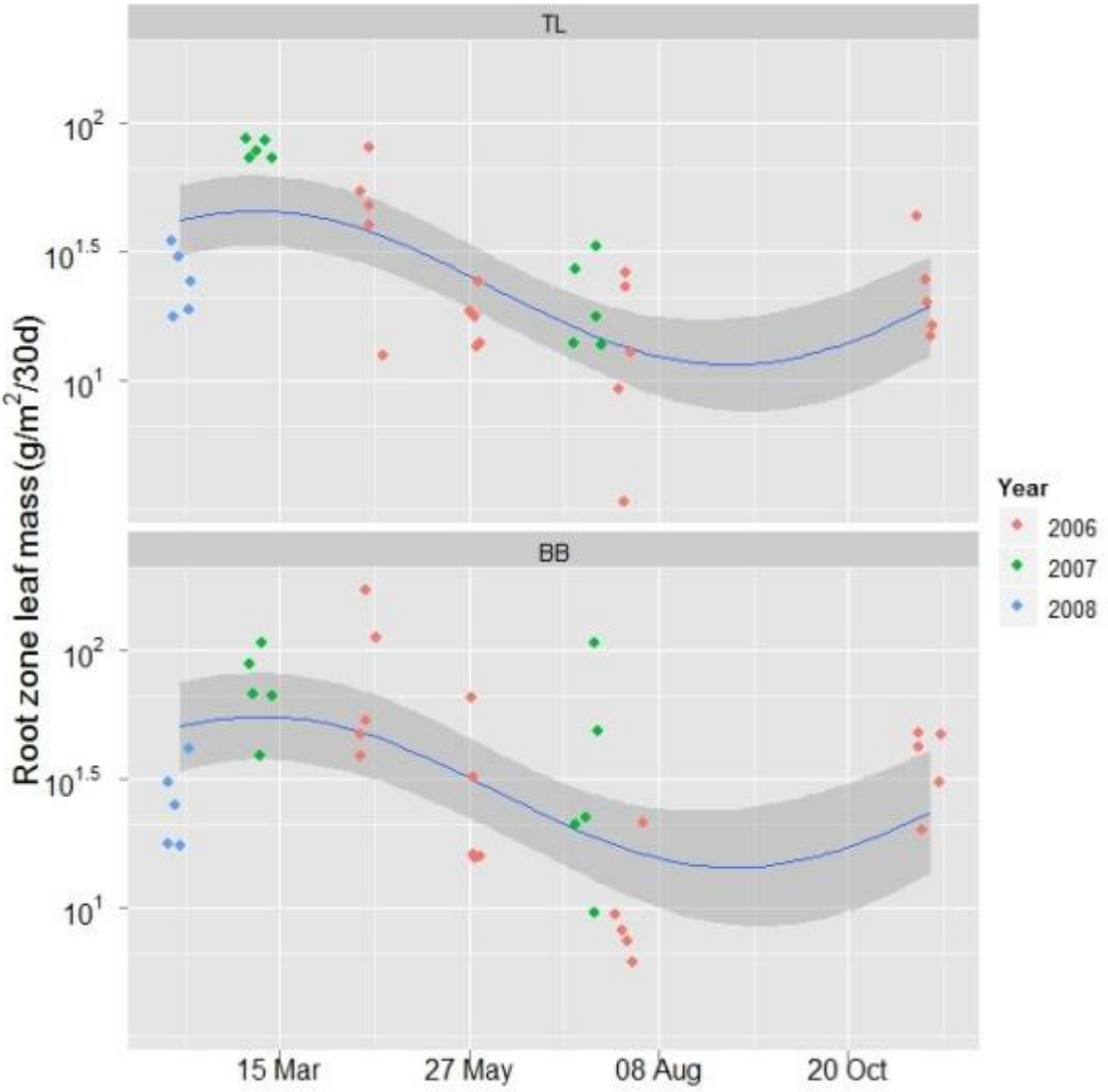


Fig. 3.12. Log_{10} leaf mass ($g.m^{-2}$) per 30 day period in the benthic root zone of the Tooms study sites. TL and BB are the upstream and downstream sites on Tooms River, respectively. Dots represent individual sediment mats (n = 5), with the year of collection indicated by the colours in the legend. The blue line shows the periodic regression trend over the study period, with 95% confidence intervals in grey.

Table 3.6 Parameter estimates from the periodic regressions of litter mass in the benthic root zone for the Tooms River sites with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the $\log_{10}$-tranformed scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the $\log_{10}$-transformed scale, and the "Date" is the date of this maximum value. (The date values have been back-transformed from the phase angle values, θ, which are not shown here).

Site	Mean	Arithmetic mean	Amplitude	Date
TL	1.36 (1.19, 1.53)	22.8 (15.5, 33.7)	0.299 (0.164, 0.741)	Mar 05 (Feb 26, Aug 01)
BB	1.45 (1.22, 1.68)	28.1 (16.7, 47.5)	0.293 (0.322, 0.887)	Mar 07 (Feb 26, Aug 11)

ANOSIM analysis showed that both the leafy and woody components of the root mat litter were significantly different between sites (Global R= 0.112, p = 0.001 and Global R= 0.076, p = 0.002 respectively). SIMPER suggested that twigs and *Leptospermum* fruit were more abundant at the upstream site, TL, with eucalypt and *Acacia* fruit more abundant at BB. Algae (chiefly diatoms) and sedge were more abundant at BB, while eucalypt and *Leptospermum* leaves were more abundant at TL. Algal abundance peaked in winter 2006, while eucalypt leaves were more abundant in summer 2007-08. *Leptospermum* leaves were least abundant in winter 2006, when discharge in Tooms River was very low.

3.4.3 Cellulose decomposition potential

Cotton strip tensile strength loss varied between and within sites, with surface strips decomposing significantly faster (ANOVA, $F_{(1, 31)}$ = 6.384, p= 0.022) at the downstream Macquarie site, IF, than at the other sites (upper panel, Fig.3.13). In contrast, buried strip decomposition was significantly faster at the downstream Tooms site, BB, ($F_{(1, 31)}$ = 13.65, p= 0.0019) than at the other sites (lower panel, Fig. 3.13. The slowest decomposition was at the upstream Macquarie site, CB for both treatment types. Buried strips decomposed more slowly at TL than at BB, while surface strips lost strength more slowly at BB than at TL.

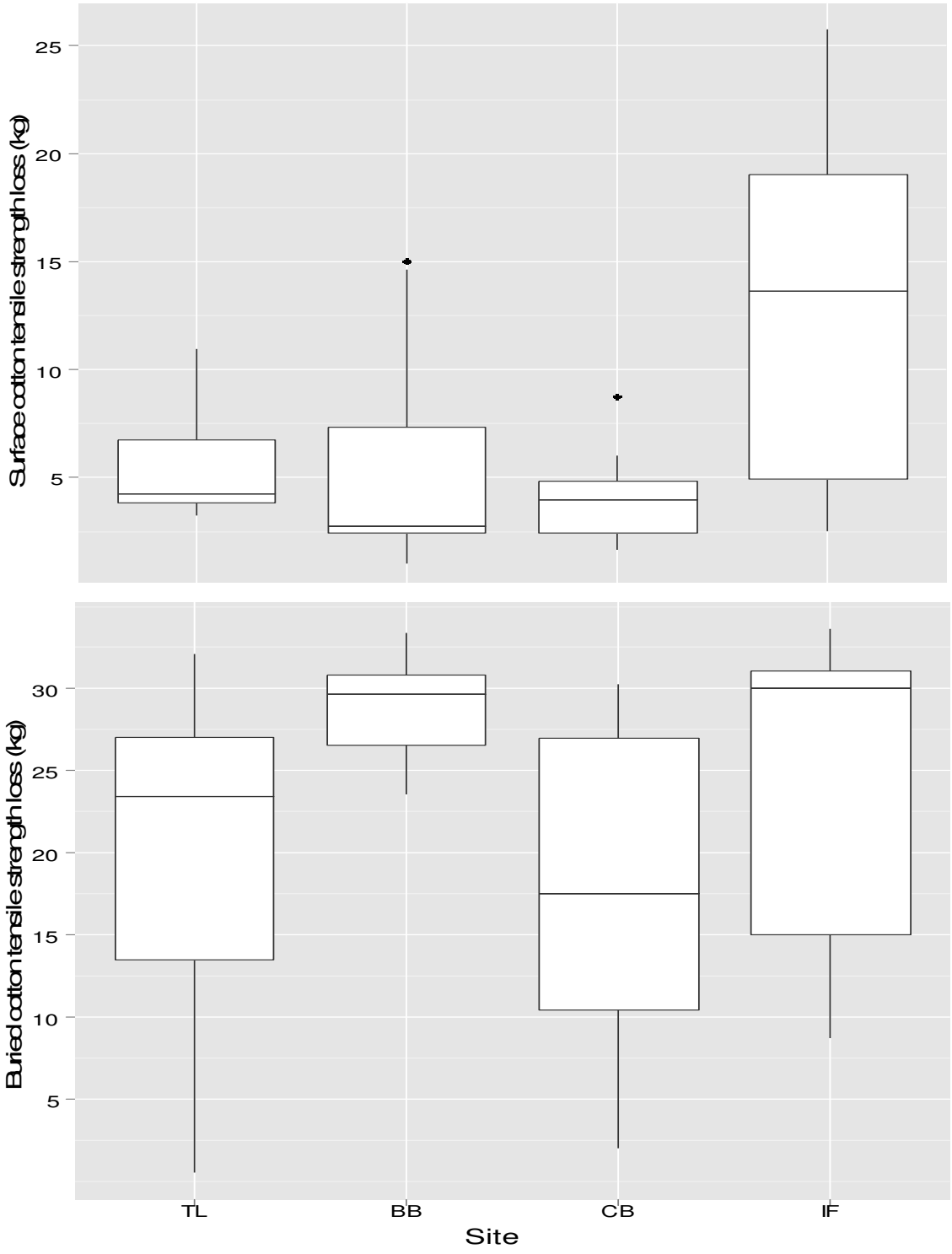


Fig. 3.13 Box plots (mean and standard deviation) of surface cotton strips (upper panel) and buried cotton strips (lower panel) tensile strength loss (kg). Note that the two panels have different y-axis scales.

3.4.4 Canopy cover

Although there was greater variation in canopy cover at the Tooms River sites than at the Macquarie sites, there was no significant difference between rivers or between sites in the percentage canopy cover over the sediment mats ($F_{(3.\ 19)}$ 1.055, p = 0.39) (Table 3.2).

3.4.5 Soil characteristics

Soil samples from BB had significantly higher moisture content (ANOVA, $F_{(1,\ 17)}$ = 9.08, p = 0.013) than the other sites, and the highest organic matter content. TL soils had significantly less OM ($F_{(1,\ 17)}$ = 6.677, p = 0.027) than the other sites (Table 3.7). Soils at TL were also more acidic than at the other sites, although the differences between the sites were not significant.

Table 3.7 Mean values of physicochemical variables of at each site, ± 1 se, showing the percentage canopy cover over the sediment mats, and the mean pH, OM content and water content of the soil samples.

Site	Canopy cover %	Soil pH	Organic matter %	Water content %
CB	67.20 ± 4.64	6.1 ± 0.27	33.90 ± 12.13	6.42 ± 2.03
IF	62.05 ± 4.74	5.7 ± 0.47	33.99 ± 13.61	9.93 ± 3.03
TL	60.55 ± 7.89	5.5 ± 0.41	28.12 ± 3.27	7.07 ± 2.67
BB	65.06 ± 7.92	6.0 ± 0.58	38.22 ± 18.32	13.56 ± 4.17

There were no significant correlations between the surface cotton strip CTSL and measured soil characteristics. However, there was a strong correlation between the mean CTSL of buried strips and the water and organic matter content of the soil samples (Table 3.8). There were no significant correlations with the percentage canopy cover above the sediment mats, or between soil organic matter content and soil water content (Pearsons r = 0.184).

Table 3.8 Pearsons correlation coefficients between mean cotton tensile strength loss and soil physicochemical variables. Strong correlations ($r \geq 0.7$) are in bold type.

Strip treatment	Canopy cover %	pH	Water content %	OM content %
Buried	-0.072	0.040	**0.991**	**0.681**
Surface	-0.485	-0.460	0.247	0.062

3.5 Discussion

Whilst it is generally accepted that the development of riparian vegetation, and thus litter accumulation, is a response to the flow regime (e.g. Nilsson and Berggren 2000; Nilsson and Svedmark 2002), it is difficult to compare findings between studies. The broad range of riparian vegetation types and species compositions both between and within rivers means that there is a highly variable response to changes in the flow regime. For example, there are many studies of *Populus* spp. in riparian zones in semi-arid zones of the USA (e.g. Stromberg *et al.* 2010). In these regions, *Populus* can be replaced by xeric species, such as *Tamarix* sp., as the groundwater increases in depth with the regulation of the flow regime. In contrast, the riparian vegetation of parts of the Murray-Darling River system in Australia is dominated by *Eucalyptus camaldulensis,* which requires regular overbank flows for seedling recruitment, and suffers dieback of mature trees when overbank flows decrease in frequency (e.g. Bren 1988). On the Murray River floodplains, invasion of the riparian zone is typically by exotic species, such as willow (*Salix* spp.) (Schulze and Walker 1997). However, these examples all relate to floodplain river systems, where geomorphic and hydraulic processes differ from those in the confined Tooms River.

There are few exotic plant species in the Tooms River riparian zone, although there are limited outbreaks of gorse (*Ulex europaeus*) at the site

near the dam. The heavy shade at this site discourages the establishment of weed species as well as the native understorey vegetation. Nevertheless, the reduction of floods with flow regulation has altered the riparian zone of both Tooms River sites, with the greatest impact on the upstream site. The stable flow regime at these sites allows larger trees, which can withstand the rare floods, to grow near the channel (Bendix and Hupp 2000; Gurnell and Petts 2002). This observation is supported by a study of eastern Tasmanian rivers by DPIPWE (2010), which included other sites on the Macquarie River. They found that mature eucalypts beside the active channel distinguished rivers with low flow variability from rivers with high flow variability.

In contrast, the riparian vegetation at the upstream Macquarie site, CB, reflects the recurrence of dramatic floods. I would expect the few seedlings which germinate in the active channel to be removed by the next flood, with high stream power maintaining an open channel. At this site, flood waters are unable to spread outside the main channel, whereas they can overflow onto the narrow floodplain at all other sites. There is an abrupt boundary between the vegetation and active channel at CB, with little fine sediment deposition. Flood resistant *Acacia* and *Leptospermum* spp. border the channel, with less resilient eucalypts beyond the reach of regular floods (Fig. 3.2). This zonation of riparian vegetation is also found at the downstream Macquarie site, IF, and has been recorded for other Tasmanian rivers with high flow variability (DPIPWE 2010).

This study suggests that flood activity can influence litter accumulation at the Macquarie River sites. The high initial litter standing stock at CB was probably due to overbank flows in the Macquarie River in August, October and December 2005, all of which would have inundated the litter collection points. The August 2005 rain event was entirely retained by the Tooms River dam. The highest discharge was 3 m^3sec^{-1} when the

dam spilled in October and December 2005, which would have produced overbank flow at TL, but not at BB (Ch. 2.7.2).

Litterfall, as measured with Astroturf® mats, was expected to be more variable at the Macquarie River sites, in response to the more variable flow regime. Contrary to expectations, riparian litter fall was higher and most variable at the Tooms River sites. This is in direct contrast to Anderson *et al.*'s (2003) experience in regulated and unregulated rivers in Colorado. The different flow regimes in the regulated Tooms and unregulated Macquarie Rivers also produced strong differences in the seasonality of riparian litter fall, resulting in the delay of peak litter fall until autumn in Tooms River. Plants in riparian zones develop in response to the flow regime (Naiman *et al.* 2005). In an unregulated system, variable water availability encourages the development of deep and extensive root systems (Scott *et al.* 2000; Shafroth *et al.* 2000). In contrast, plants that develop under a low variability regime may have shallow roots and be subject to water stress under unusually low water levels (Scott *et al.* 1999). The earlier onset of litter fall recorded at the Macquarie sites is likely to be in response to seasonal water stress (Campbell and Fuchshuber 1994), while leaf fall at Tooms River was delayed until irrigation demand decreased at the end of summer. Peak litter fall at IF was later than that at the upstream Macquarie site, CB. This could indicate that the riparian vegetation at IF, where the study reach completely dried in summer, is better adapted to seasonal drought than that at CB, where the channel retains some remnant pools. Alternatively, the broadwater pool upstream of IF may supply a reliable source of groundwater to the riparian vegetation at this site, delaying the onset of drought stress.

The upstream Tooms River site (TL) showed greater seasonal variation in litter accumulation than the downstream site, despite Campbell *et al.*'s (1992) proposal that consistent water levels should reduce seasonality in the riparian zone. The riparian vegetation at this site includes species

usually found in higher rainfall areas (Figs. 3.14, 3.15), including ferns and mosses. Water abstraction for irrigation was prohibited when the lake capacity was drawn down to low levels. This produced lower than 'normal' summer flows in Tooms River, which is likely to have produced drought stress in the riparian vegetation at TL (Dr. N. Davidson, University of Tasmania, pers. comm.).

The significantly lower flows in 2007 (Ch. 2.6.2) also increased litter accumulation on the mats in the benthic root zone of Tooms River, with limited fluvial transport and a narrower wetted channel.

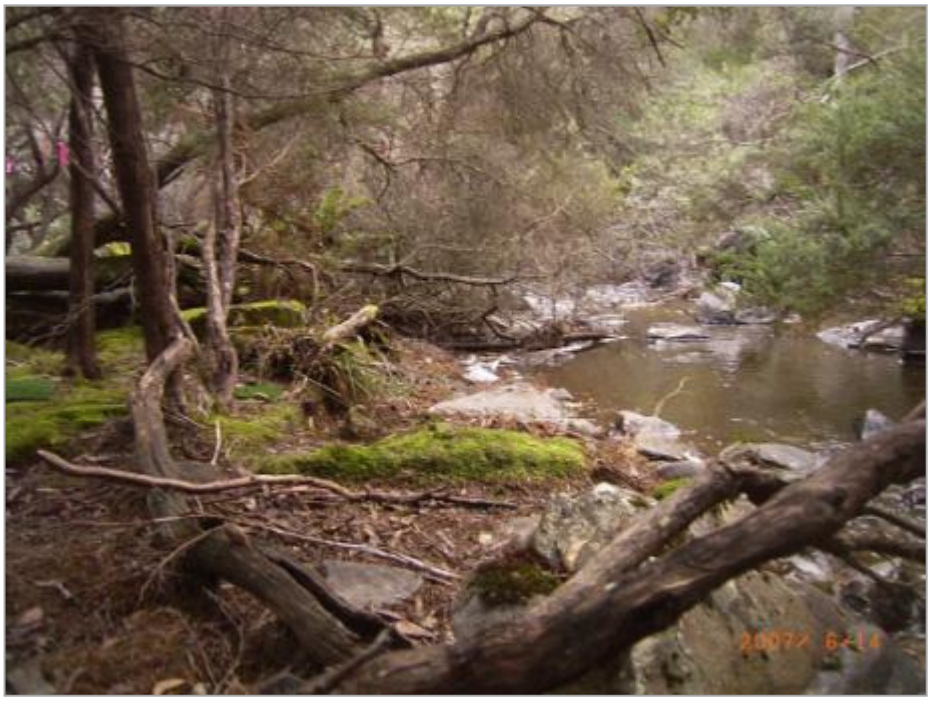


Fig. 3.14 Riparian zone at the upstream Tooms River site, TL, with moss beds and abundant woody debris.

Fig. 3.15 Riparian zone at the upstream Tooms River site, TL, with the fern *Blechnum nudum* and with desiccated biofilms covering the ground surface after the floods in September 2009.

Annual riparian litter fall was low at all sites compared to other published Australian studies, although disparity between litter trap type and placement makes comparisons between studies difficult. McIvor (2001) measured similar litter levels (72-127 $g.m^{-2}$) in suspended mesh traps in a 3 year study of eucalypt woodlands in semi-arid northeast Queensland. Lee and Correll (1978) recorded higher mean annual litter fall levels (233 $g.m^{-2}$) in a dry sclerophyll forest in South Australia, while 329 $g.m^{-2}$ annual litter fall was recorded in a dry eucalypt forest near Canberra, ACT (Crockford and Richardson 1998). However, litter fall can differ between forest sites and riparian zones, with higher litter fall in the riparian zone than either the forest or stream bed (Campbell *et al.* 1992). By contrast, Thomas *et al.* (1992), using suspended mesh bags, collected less eucalypt litter in the riparian zone than in an adjacent forest in the ACT. The artificial turf mats used in the current study potentially collected more small leaves than suspended litter traps, but some larger leaves may have been blown off the mats. However, this would have

been unlikely to produce the significant differences found between sites or rivers, because the mats were generally protected from strong winds.

The relationship between litter decomposition and soil moisture levels can be described by a quadratic function of the form $f(x) = ax^2 + bx + c$ with maximum decomposition rates in moderately damp soil (Ise and Moorcroft 2006). Decomposition rates are reduced by low microbial activity in dry soils, and anaerobic conditions in saturated soils (Williams and Gray 1974; Davidson and Janssens 2006). For example, Pinna and Basset (2004) showed that leaf litter decomposition was faster at moister sites than at dry sites. On this basis, the abundant rotting wood in the riparian zone at TL was predicted to be a sign of high soil moisture levels and moderately high decomposition rates (Table 3.1). However, this may actually be a sign of slow decomposition, supported by the presence of dense *Leptospermum* root mats in the Tooms River channel. These may indicate anoxic conditions at these sites, since adventitious roots are typically produced by vegetation adapted to anoxia (Naiman and Décamps 1997). Contrary to expectations, soil moisture was lower at TL than at either BB or IF, potentially indicating a stronger reliance of riparian vegetation on stream flow at TL than at the other sites. Cellulose decomposition potential showed that surface cotton strips decomposed most rapidly at IF, and buried cotton strips lost less tensile strength at TL than at either BB or IF. This was reflected in soil organic matter content, which was lower at TL than at any other site. The lower percentage of soil organic material at this site may indicate limited replacement of soil nutrient levels (e.g. Qualls and Haines 1992), combining with heavy shade to inhibit seedling germination and growth (Withers 1979). This hypothesis could be tested by assessing the age structure of the riparian vegetation, and the percentage of soil organic material at a number of sites along a gradient of shade levels with increasing distance from the Tooms River dam.

Interestingly, the same detrital components contribute to the differences between upstream and downstream sites on both rivers. Sedge and *Juncus* blades and *Acacia* pods are more abundant at both of the downstream sites. This may relate to the close proximity of the sites, but may also reflect a common land-use history. Both BB and IF are on alluvial floodplains, where the riparian vegetation has been modified by grazing. This has reduced the cover of leafy shrubs at both sites, allowing establishment of graminoids such as *Lomandra longifolia* and *Poa labillardierei*. The greater disturbance to these sites may have led to increased dominance of *Acacia* species, which are recognised as disturbance specialists (Adams and Attiwill 1984).

3.6 Conclusion

The riparian zone of Tooms River has been modified by flow regulation, consistent with Pett's (1980) prediction of second-order effects. This influences the accumulation and cycling of leaf litter. Figure 3.1 conceptualised the movement of riparian and benthic litter under low and high flows, while Table 3.1 summarised the likely influence of the modified riparian zone on riparian litter accumulation and decomposition.

As predicted, mean litterfall was highest at the Tooms River sites, but peak litterfall was delayed until autumn at these sites, in contrast to the summer litter fall at the Macquarie sites, and as reported in other Australian studies (e.g. Campbell and Fuchshuber 1994). *Acacia* and *Leptospermum* leaves were expected to be more abundant at the Macquarie sites, due to the abundance of these plant species in the riparian zone, but these leaves were surprisingly abundant at the downstream Tooms site, BB. *Eucalyptus* leaves were expected to be most abundant at the downstream Tooms site, BB, but were most abundant at the upstream Tooms site, TL, in contrast to the prediction that the dense riparian vegetation would suppress eucalypt leaf abundance. Litter decomposition, as assessed by cellulose decomposition potential,

was expected to be highest at the Tooms River sites, but was surprisingly high for the downstream Macquarie site, IF (Fig. 3.13). Cellulose decomposition was similar at the two upstream sites, CB and TL, where soil moisture levels were lowest.

As predicted, the drought had similar effects on each river, with litter fall higher at all sites in 2007 than in 2006, when flow was lower in both rivers. The reduction in discharge in Tooms River with the prevailing drought decreased the width of the wetted channel (Chapter 2), so that more litter accumulated on the mats in the root zone than would have accumulated under 'normal' flow levels. High flows were rare in the Macquarie River during the study period, so that less litter accumulated in the riparian zone than was present in the initial standing stock.

Both the upstream Tooms site and the downstream Macquarie site are affected by flow discontinuity (Ward and Stanford 1983b) created artificially by the dam in Tooms River and naturally by the broadwater in the Macquarie River, which results in some similarities between these sites. For example, the total mass and woody mass of the initial standing stock of riparian litter were more similar between IF and TL than with the paired sites on the same river, although the components of the woody mass were quite different (Fig. 3.10).

The study sites were matched by topographic positions in each river. It is likely that the original riparian vegetation of Tooms River was similar to that of the Macquarie sites, with a shrubby riparian zone, distinct from the surrounding dry eucalypt woodlands, as is common to other rivers in this low rainfall area (DPIPWE 2010). However, the riparian vegetation of Tooms River and the upstream site in particular, has been heavily modified, with consequences for the abundance, seasonality and composition of riparian plant detritus, and potentially for the availability of allochthonous and autochthonous benthic resources.

Future research should focus on establishing whether the patterns of riparian litterfall observed at the Macquarie sites are typical of other unregulated eastern Tasmanian rivers, or specific to this river, and how large an influence the drought had on litter dynamics. The role of decomposition in litter accumulation, and hence in nutrient cycling, was assessed with a single cellulose decomposition potential assay, which suggested that decomposition rates were higher at the two downstream sites. Extension of this technique, coupled with leaf litter decomposition trials, across multiple seasons may establish a consistent pattern in litter decomposition across these sites, but may also detect strong seasonal differences, relating to variation in microbial activity, seasonal abundance of macroinvertebrates, the flow regime or specific site characteristics.

Chapter 4 Benthic resource dynamics in response to flow regulation

4.1 Abstract

Riverine food webs are fuelled by allochthonous organic material and autochthonous biofilms. Regulation of the flow regime can influence the structure and species composition of the riparian vegetation, impacting on the availability and abundance of benthic resources. Allochthonous and autochthonous resources were compared between a regulated and an unregulated river in eastern Tasmania. The heavy shade and turbidity of the regulated Tooms River were expected to suppress autotrophic biofilms, with high levels of allochthonous material contributing dissolved organic carbon to the heterotrophic microbial loop. Although benthic detritus and biofilms were more abundant in the regulated river, autotrophic diatoms and cyanobacteria dominated, in contrast to the filamentous algae and vascular macrophytes of the unregulated Macquarie River. Unexpectedly, while biofilm abundance varied seasonally in the unregulated Macquarie River, there was no seasonal trend in Tooms River. The reversed seasonality of flow in Tooms River was not reflected in reversed biofilm seasonality.

4.2 Introduction

There are two main sources of the organic material that fuels riverine food webs. Riparian vegetation contributes allochthonous detritus, while autochthonous organic material is produced by photosynthetic algae and macrophytes within the stream (Dobson and Frid 1998). Smaller forested streams are thought to be heterotrophic, with allochthonous leafy detritus contributing most of the energy base (Benfield 1997), while there is some evidence for increased contributions of autochthonous resources in larger river segments downstream (e.g. Robertson *et al.* 1999). The amount of leafy detritus available as a resource for benthic

biota is a reflection of riparian litter inputs (Bilby and Likens 1980), but is also strongly controlled by hydrological factors (Webster *et al.* 1999).

Benthic algae may underpin the food webs of many Australian river systems, because autochthonous productivity may be more important than terrestrial sources in larger rivers (Bunn *et al.* 2003). Algae and biofilms (periphyton) have an important influence on aquatic food webs (Minshall 1978), by converting inorganic materials (Hoellein *et al.* 2010), nutrients (Lock *et al.* 1984) and sunlight to food resources (Biggs 1996), which are consumed by benthic invertebrates (Gregory 1983). Bacteria and fungi have major roles in the decomposition of allochthonous detritus (Bärlocher and Kendrick 1974; Chergui and Pattee 1991; Baldy *et al.* 1995). A river's flow regime influences the abundance and community composition of algae and biofilms, in combination with physicochemical factors such as nutrient availability, and the density and structure of the riparian vegetation (Biggs and Close 1989).

4.2.1 Autochthonous resources

Biofilms are a mixture of heterotrophic fungi and bacteria, autotrophic algae, diatoms and cyanobacteria, and inorganic particles (Lamberti and Steinman 1997; Hoellein *et al.* 2010) in a polysaccharide matrix (Wetzel 1983). These grow on leaf litter, wood, stones and other substrates in streams (Burns and Ryder 2001). Photosynthetic green algae (Chlorophyta), diatoms (Bacilliariophyta) and Cyanobacteria dominate in high light environments (Lock *et al.* 1984; Peterson 1996). Although Richardson (1983) proposed that cyanobacteria and diatoms would be more important than green algae in low light environments, Albariño *et al.* (2008) showed that fungi (aquatic hyphomycetes) were more likely to be found in shaded environments and that bacteria could thrive in light or shaded environments.

Flow regulation can influence biofilm abundance and species composition (Biggs 1996; Chester and Norris 2006), linked to the

frequency and magnitude of disturbances (Bayley 1991; Mosisch and Bunn 1997). A variable flow regime is likely to select for biofilms which can rapidly respond to changing conditions (Peterson 1996). For example, Growns and Growns (2001) showed that different diatom species occurred in regulated and unregulated streams of the Hawkesbury – Nepean River system in Australia. Biofilms are also influenced by temperature, light, nutrient availability and invertebrate feeding activity (Hynes 1970a; Hynes 1970b). Many studies have shown that the reduction in turbidity with flow regulation increases the abundance of filamentous algae below impoundments (e.g. Angradi 1994; Vinson 2001), although the majority of these studies are of large dams for hydro-electric generation. However, Nichols *et al.* (2006) also recorded more filamentous algae and periphyton at sites below water supply impoundments than at reference sites on the Cotter River in the Australian Capital Territory. In contrast, cyanobacteria dominated biofilms below the Hume Weir on the Murray River (Baldwin *et al.* 2009).

4.2.2 Allochthonous resources

The accession of plant detritus to the benthos is a function of the composition of the riparian vegetation and the stream morphology, both of which influence lateral and vertical inputs (Fig. 3.1), and downstream litter transport (Abelho 2001). In Australian streams, leaves or leaf fragments can make up more than 50% of the total input (Campbell *et al.* 1992), with the remainder consisting of flowers, fruit, bark and woody debris.

Leaf litter must be retained in the stream reach for it to be accessible to benthic organisms (Speaker *et al.* 1984). The leaf surface is initially colonised by fungi and bacteria, before abrasion and invertebrate feeding break the material down into smaller fragments (Boling *et al.* 1975). The rate of decomposition varies with stream temperature, microbial activity and the presence or absence of shredding invertebrates (Graça *et al.* 2001). The level of nutrient enrichment within the stream can also

influence organic material (OM) breakdown rates (Molinero *et al.* 1996), although this is also influenced by the morphology and chemical composition of individual leaf species (Abelho 2001).

In temperate Australian eucalypt forests, the period of highest litter input tends to be in summer, when stream flow is low, which leads to the accumulation of leaf litter in the benthos (Bunn 1986). The reversed seasonality of flow in a river regulated for irrigation supply is likely to impact on the retention, abundance and decomposition of benthic detritus, because peak litterfall coincides with the highest flows rather than the lowest flows (Watkins *et al.* 2010). In the longer term, river regulation can interact with individual site characteristics and change the structure and composition of the riparian vegetation, which, in turn, may influence both autochthonous and allochthonous resource availability.

Table 4.1 summarises the riparian conditions and in-stream conditions of the sites in this study and, based on the foregoing literature, proposes some qualitative expectations about the relative differences between them in terms of the in-stream resources examined in this study.

Table 4.1 Potential influences of site characteristics on resource abundance.

Variable	Upstream Macquarie (CB)	Downstream Macquarie (IF)	Upstream Tooms (TL)	Downstream Tooms (BB)
Light access	Open canopy	Open canopy	Closed canopy	Open canopy
Orientation	ENE-WSW	E-W	ENE-WSW	SSE-NNW
Substrate	Cobbles, boulders & bedrock	Cobbles	Cobbles, boulders & bedrock	Cobbles, boulders & bedrock
Morphology	Constrained reach	Constrained reach	Constrained reach	Constrained reach
Slope %	1.79	0.59	0.95	1.33
Nutrients	Low	Low	Enriched	Enriched
Temperature (Min –Max ^{o}C)	3.2 – 21.9	4.6 – 22.4	4.5 – 22.3	4.6 – 22.6
Potential impacts	Forestry	Agriculture	Impoundment	Agriculture
Expectations	Moderate algal biomass, low bacteria and fungi, moderate OM	Highest algal biomass, low bacteria and fungi, lowest OM	Lowest algal biomass, high bacteria and fungi, high OM	Moderate algal biomass, moderate bacteria and fungi, highest OM

Although Tooms Lake is shallow and does not stratify, the thermal inertia typical of large water bodies was evident in the water temperature regime of the Tooms River sites, determined by spot temperature readings at each site. In winter, Tooms River was up to 3.1 ^{o}C (mean 1.7 ^{o}C) warmer than the Macquarie. However, in summer the pools in the Macquarie River were up to 5 ^{o}C (mean 3.4 ^{o}C) warmer than the permanent flow in Tooms River. The upstream Macquarie site, CB, was always 0.1 – 2.8 ^{o}C (mean 1.2 ^{o}C) colder than the downstream site, IF. In contrast, the upstream Tooms site, TL, was 0.8 – 2.9 ^{o}C (mean 2.1 ^{o}C)

colder than the downstream site, BB, in summer, but up to 0.5 °C warmer in winter.

Overall, the site on Tooms River immediately downstream of the dam (site TL) was expected to deviate most strongly from the other study sites. At TL, low light levels, produced by highly turbid water released from the dam and by shading by the riparian vegetation, were expected to suppress photosynthetic algae and promote microbial biofilms, as Albariño *et al.* (2008) found in Andean – Patagonian streams. Microbial activity was expected to accelerate decomposition of leafy detritus in the regulated river, as reported for other systems with moderately high nutrient levels (e.g. Gulis *et al.* 2006). It was hypothesised that biofilms would be more abundant in Tooms River because the reduced peak flows (see Chapter 2) would result in fewer scouring events (e.g. Voelz and Ward 1989; Burns and Walker 2000b), and increased decomposing leaf litter biomass could produce more dissolved organic carbon (DOC) to supply labile carbon to the biofilms (Romaní *et al.* 2004). In contrast, the more open canopy of the unregulated Macquarie River was expected to promote autotrophic algae over heterotrophic biofilms (Lock *et al.* 1984).

Leaf litter was also expected to be more abundant in Tooms River, with high litter input from the overhanging riparian vegetation. Leaf litter tends to move downstream with water flow unless caught by retention structures (Mathooko 1995), so it was anticipated that the greater volume of woody debris observed in Tooms River would increase benthic litter retention, and hence abundance. Steart *et al.* (2002) and Quinn *et al.* (2007) showed that the buoyancy of different leaf types affected their transport and retention in response to turbulence. Therefore, the buoyancy of leaves was also expected to influence their abundance in the benthos, with larger leaves more abundant than small leaves in Tooms River.

4.3 Methods

4.3.1 Autochthonous resources

Algae and biofilms were sampled by randomly collecting nine small rocks (mean surface area 0.015 m^2 ± 0.0045, up to 150 mm diameter) at each site at quarterly intervals, commencing March 2006. Collections were made quarterly to assess seasonal variation in biofilm abundances. The water velocity and depth from which rocks were collected were not measured, but the depth was less then 450 mm on each occasion. Each rock was immediately placed into a sealed ziplock bag with a small amount of river water and stored on ice for the return to the laboratory. Each rock was frozen (-18 ^oC), until analysis, at room temperature, up to a maximum of 6 weeks after collection. All laboratory analyses were conducted under subdued natural lighting, to prevent degradation of chlorophyll (e.g. Biggs and Kilroy 2000).

Each rock was scraped with a scalpel blade and scrubbed with a toothbrush to remove the attached algae, which was washed into 200 mL distilled water. Samples containing filamentous or globular algae were homogenised with a motorised rotating blade (CAT X620, M.Zipperer: Staufen-Etzenbach), to obtain accurate sub-sampling (Biggs and Kilroy 2000). Homogenisation was shown to have no significant effect on chlorophyll extraction efficiency in ethanol (Wasmund *et al.* 2006). A 50mL aliquot of algal slurry was used for chlorophyll extraction and 100 mL to calculate biofilm ash free dry mass (AFDM). The remaining 50 mL was preserved with Lugol's iodine solution for future cell counts.

4.3.1.1 Rock surface area

The surface area of each rock was measured using the aluminium foil method of Steinman *et al.* (2006). The algae covered surface of each rock was wrapped in aluminium foil, without overlap, with excess foil removed with scissors. The foil was dried (1 h, 50 ^oC) then weighed to the nearest 0.001g. The mean mass of six 100 x 100 mm pieces of clean aluminium

foil was used as a reference. Rock surface area (A_r) in square metres was calculated using the formula:

$$A_r = \left(\frac{A_k}{W_k} \right) x W_{rf}$$

where A_k = known area of 100 x 100 mm piece of aluminium foil, W_k = known mean weight of 100 x 100 mm foil (g), and W_{rf} = weight of foil from rock (g) (Steinman *et al.* 2006).

The river bed substrate, reported in Table 4.1, was assessed by site inspections and from photographs taken at low flows.

4.3.1.2 Biofilm AFDM

To calculate biofilm ash free dry mass, 100 mL of algal slurry, or a measured fraction thereof, was filtered through pre-ashed (2 h, 400 °C) and pre-weighed Whatman GF/F glass filters (0.7 µm pore). Each filter was dried (48 h, 40 °C), weighed for dry mass, then ashed (4 h, 400 °C). AFDM was calculated using the formula:

$$AFDM(g.sample) = \frac{(W_{dry} - W_{ash}) x V_1}{V_s}$$

Where W_{dry} = dry mass of sample minus mass of filter (g), W_{ash} = mass of sample minus mass of filter after ashing, V_1 = sample volume (L) and V_s = volume of sub-sample (L) (Biggs and Kilroy 2000).

Ash free dry mass per square metre of substrate was calculated as:

$$AFDM\ \left(g.m^{-2}\right) = \frac{AFDM}{A}$$

where *AFDM* is ash free dry mass (g./sample) and *A* is the rock surface area (m^2).

4.3.1.3 Chlorophyll a

Chlorophyll *a* extraction generally followed the protocols of Biggs and Kilroy (2000) for freshwater periphyton, based on the procedures recommended by Sartory and co-workers (1982; 1984). For the first sample round, a 50 mL sub-sample of algal slurry was collected on Whatman GF/F glass filters (0.7 µm pore), as for algal biomass. The filters were sealed in foil-wrapped test tubes, with 10 mL aqueous 90% ethanol as extractant. Ethanol was preferred for extraction due to its superior extraction ability for an unknown biofilm taxonomic composition (Wasmund *et al.* 2006) and the low toxicity and cost of ethanol in comparison to methanol or acetone extraction (Ritchie 2006). Chlorophyll was extracted in a dark water bath at 78 ^{o}C for 5 minutes (Biggs and Kilroy 2000), then for the balance of 24 hours at room temperature (18 ^{o}C) (Sartory and Grobbelaar 1984). A 3 mL aliquot of supernatant was transferred to a polystyrene cuvette. Spectral absorbance was measured in a UV-120-02 spectrophotometer (Shimadzu, Kyoto, Japan), with a 1 cm light path and 1 nM bandwidth, zeroed with 90% ethanol. Maximum absorbance at 665 nM was corrected for turbidity by subtracting absorbance at 750 nM (Ritchie 2006, 2008). Absorbances were corrected for phaeophytin content by subtracting the absorbance after acidification with 3 µl of 1M hydrochloric acid (Sartory and Grobbelaar 1984). Phaeophytin absorbance showed a strong positive correlation with chlorophyll *a* absorbance for all collection rounds ($r^2 > 0.9469$).

Collection of the algal slurry on filters was replaced by concentration by centrifugation (Ritchie 2006) as detailed below, for the second and subsequent sample rounds, due to the significant time and additional cost involved in filtering. A pilot study showed that while centrifugation slightly increased chlorophyll extraction efficiency, there was no significant difference between chlorophyll concentration of the algal

slurry by filtering and concentration by centrifugation (ANOVA $F_{(1, 36)}$ = 0.3018, p = 0.59).

A 50 mL fraction of algal slurry was centrifuged (Megafuge 2.0, Kendro Laboratory Products, Germany) for 10 minutes at 3000 rpm (1580 x *g*). After removal of the supernatant, 10 mL of aqueous 90% ethanol (Sartory and Grobbelaar 1984) was added to the tube. The centrifuge pellet was broken up with a glass rod and sonicated for 1 minute. Chlorophyll was extracted in hot ethanol as detailed above. After extraction, samples were centrifuged (5 min, 2500 rpm (1350 x *g*)) to remove chlorophyllides (Ritchie 2006) and reduce turbidity before spectral absorbance was read from a 3 mL aliquot of the supernatant.

Chlorophyll *a* in absorbance units was converted to milligrams per square metre of rock surface:

$$Chl\ a = \frac{28.66\,(E_{665\,b} - E_{665\,a})\,x\,V_{ext}\ \ x\,V_1}{A\,x\,V_s}$$

where *Chl a* is chlorophyll *a* concentration (mg. m^{-2}); 28.66 is the chlorophyll *a* absorbance coefficient in 90% ethanol (Sartory and Grobbelaar 1984), based on the chlorophyll *a* specific absorption coefficient of 83.4 $g^{-1}.L^{-1}.cm$ (Wintermans and De Mots 1965) and an acid ratio of 1.72 for chlorophyll *a* in ethanol (Sartory 1982). E_{665b} is the spectral absorbance at 665 nm minus absorbance at 750 nm before acidification; E_{665a} is spectral absorbance at 665 nm minus absorbance at 750 nm after acidification; V_{ext} is the volume of ethanol (L) used in extraction; V_1 is the full sample volume; A is the area of rock sampled (m^2); and V_s is the subsample volume (Biggs and Kilroy 2000).

4.3.1.4 Autotrophic Index

The total organic content of biofilms is determined by ash free dry mass, while chlorophyll *a* represents the autotrophic component. The autotrophic index (AI) indicates the degree of autotrophy or heterotrophy.

The Autotrophic Index was calculated for each sample (APHA 2005) as:

$$AI = \frac{AFDM\ (mg.m^{-2})}{Chlorophyll a\ (mg.m^{-2})}$$

An AI of up to 100 indicates an algal dominated system, whilst indices greater than 400 indicate a system dominated by heterotrophy or high concentrations of organic detritus (Weber 1973; Collins and Weber 1978; Biggs and Hickey 1994).

4.3.2 Vascular macrophytes

Vascular aquatic macrophyte abundance was not quantified in this study, but qualitative differences were observed between rivers and sites. These observations are reported (Section 4.4.2) to allow comparisons with findings reported in other studies.

4.3.3 Suspended organic material

One litre water samples were collected at each site when sampling was undertaken for other biotic components of the project (Sections 4.3.1, 4.5.3.1). Suspended organic material was collected on pre-ashed, pre-weighed Whatman GF/F filters (0.7 µm pore), dried (24 h, 40 ^{o}C) and ashed (4 h, 550 ^{o}C). Suspended organic material was calculated as the difference between dry mass and ash mass.

4.3.4 Dissolved nutrients

One hundred mL water samples were collected in acid-washed bottles from each site when sampling for other variables, transported on ice to the laboratory and frozen (-18 ^{o}C) until analysis. Filtered samples were analysed for total organic carbon, and total dissolved nitrogen and phosphorus by APHA method 4500, at the NATA accredited Analytical Services Tas laboratory at New Town, Tasmania. Additional nutrient data for Tooms River were taken from a quarterly water quality monitoring programme undertaken by the Tasmanian Department of

Primary Industries, Parks, Water and Environment (WIST 2010). Analysis of variance was used to test for significant differences between sites or rivers.

4.3.5 Allochthonous resources

4.3.5.1 Leaf buoyancy

The movement and accumulation of leaf litter is likely to be affected by variation in the buoyancy of different leaf species (Steart *et al.* 2002). The flotation times of *Acacia mucronata, Leptospermum lanigerum*, *Eucalyptus pulchella* and *E. viminalis* leaves, the main components of benthic leafy detritus at these sites, were assessed in a laboratory trial. Leaves were fresh and naturally abscised, and air dried to constant mass.

The trials were established in 500 x 350 mm PVC containers, each containing 90 mm deep tap water at 15 ^{o}C. The effect of turbulence on leaf buoyancy was examined with 3 different surface flow regimes – still water, low flow (~ 2.5 cm^2. sec^{-1}) and a moderate flow (~ 10 cm^2. sec^{-1}) regime, as measured with a portable flow meter (Schiltknecht Messtechnik AG Mini Air 20: Gossau, Switzerland). Flow was continuously generated with compressed air injected by needle valves, so that the leaves circulated freely within each container. One hundred leaves of each species were tested in each flow regime, with *Acacia* and *E. pulchella* leaves randomly divided into 2 sets of 50 leaves to avoid clumping. *Eucalyptus viminalis* leaves were randomly divided into 4 sets of 25 leaves. Leaves were carefully scattered onto the surface of each container. The number of leaves of each species remaining floating was recorded daily for the first 15 days, then at weekly intervals for the remainder of the experiment (Steart *et al.* 2002). The still water experiment was discontinued at 100 days, at which time most leaves remained afloat and *E. viminalis* leaves were beginning to decompose. Data were analysed using the *survival* package (Therneau 2009) in R

2.11.1, employing the Kaplan-Meier estimate. Goodness of fit Chi-squared tests examined differences in flotation times between leaf species.

4.3.5.2 Benthic organic matter

Nine samples of benthic organic matter (BOM) were randomly collected with a kick net (350mm x 250 mm opening, 250 µm mesh) at each site at quarterly intervals, commencing January 2006, with an additional round (Round 7) collected after a spate in August 2007. The substrate was cleared of larger rocks after placing the net downstream, then disturbed by kicking at the substrate for 20 seconds, so that BOM was carried into the net by the water flow. The net contents were transferred to a clean ziplock bag and preserved with 70% ethanol. As flow in the Macquarie River sites was very low for most of the study period, organic matter was also collected from the dry river bed whenever there was insufficient water to collect nine kick samples. Rocks were removed from a standardised 300 x 300 mm area and rinsed over a white tray. All OM was manually collected from this area, down to a level considered equivalent to kick sampling. This material was processed as for the benthic kick samples.

In the laboratory, litter was rinsed into nested 500 µm and 65 µm sieves. The fine fraction (< 500 µm) was dried (48 h, 40 ^{o}C) and weighed to the nearest 0.01 gm, then ashed (4 hours, 550 ^{o}C) to determine the inorganic fraction of the samples. Plant material was dried (48 h, 40 ^{o}C), weighed and processed as for riparian litterfall (see 3.3.1.3). The state of decomposition of the leaf material in each sample was visually assessed using the following ordinal scale: 1 = freshly abscised leaves; 2 = mostly full leaves, some fragments; 3 = equal proportions of full leaves and leaf fragments; 4 = a few full leaves, mostly fragments; 5 = only leaf fragments.

4.3.5.3 Cellulose decomposition potential

Benthic cellulose decomposition potential was measured, in summer 2007-2008, using the same methods as for terrestrial cellulose tensile strength loss (see 3.3.2.1), except that cotton strips were enclosed in mesh bags, and retrieved strips were rinsed in clean water before air-drying.

Individual cotton strips were inserted into either coarse mesh bags (6 mm mesh), which allowed invertebrate access, or fine mesh bags (500 µm mesh), which excluded macroinvertebrates. Nine strips were used at each site for each mesh type. Three coarse mesh bags and three fine mesh bags were alternately attached to a 3 mm nylon cord with monofilament fishing line. Three cords were randomly deployed at each site, secured with steel pegs, with bag lines anchored to the benthos with cobbles to replicate the location of leaves in the benthos. Handling effects were assessed by dipping a line with 3 fine mesh bags and 3 coarse mesh bags in the water at each site, then immediately sealing the entire set of bags in a ziplock bag for transfer to the laboratory.

4.3.6 Statistical methods for the survey data

Periodic regression was used to describe trends over the annual cycle for chlorophyll *a*, ash free dry mass and benthic organic material, as detailed for riparian litter fall (see 3.3.1.4) since cyclical, seasonal changes are usually over a year with these variables.

A model was initially fitted for each dependent variable that included site (4-level factor) and its interactions with the periodic terms, but there was always at least one significant interaction. Therefore separate regressions were conducted for each site, with parameter estimates and standard errors computed and tabulated for each significant term.

In addition, the SIMPER (similarity of percentages) function in PRIMER 6.1.9 (PRIMER-E Limited 2007) separately compared the abundance of

the leafy and woody components of the benthic OM samples, with river status (regulated or unregulated) and individual sites as factors. Data were log-transformed before analysis to normalise variances.

4.4 Results

4.4.1 Autochthonous resources

4.4.1.1 Biofilm AFDM

Biofilm mass, as measured by AFDM, was significantly higher at the Tooms River sites than the Macquarie sites (ANOVA $F_{(3, 276)} = 3.563$, $p = 0.0147$). Table 4.2 shows that there was significant seasonal variation in biofilm mass at both Macquarie sites, but no seasonal variation at either of the Tooms sites.

Table 4.2 Significance of seasonal variation in biofilm mass at each site. TL and BB are the upstream and downstream Tooms sites, and CB and IF are the upstream and downstream Macquarie sites, respectively.

Site	$F_{(1, 63)}$	p
TL	1.49	0.232
BB	1.12	0.332
CB	6.39	0.003
IF	9.19	< 0.001

Peak biofilm abundance at the upstream Tooms site, TL, was seasonally opposed to that of the Macquarie sites (Fig. 4.1, Table 4.3). Peak biofilm abundance was offset between the two Tooms River sites and between the two Macquarie River sites and generally highest at times of lowest flow. Biofilm mass was higher at the downstream Macquarie site, IF, than at the upstream site, CB, on most sampling occasions, but was always more abundant at TL than at BB.

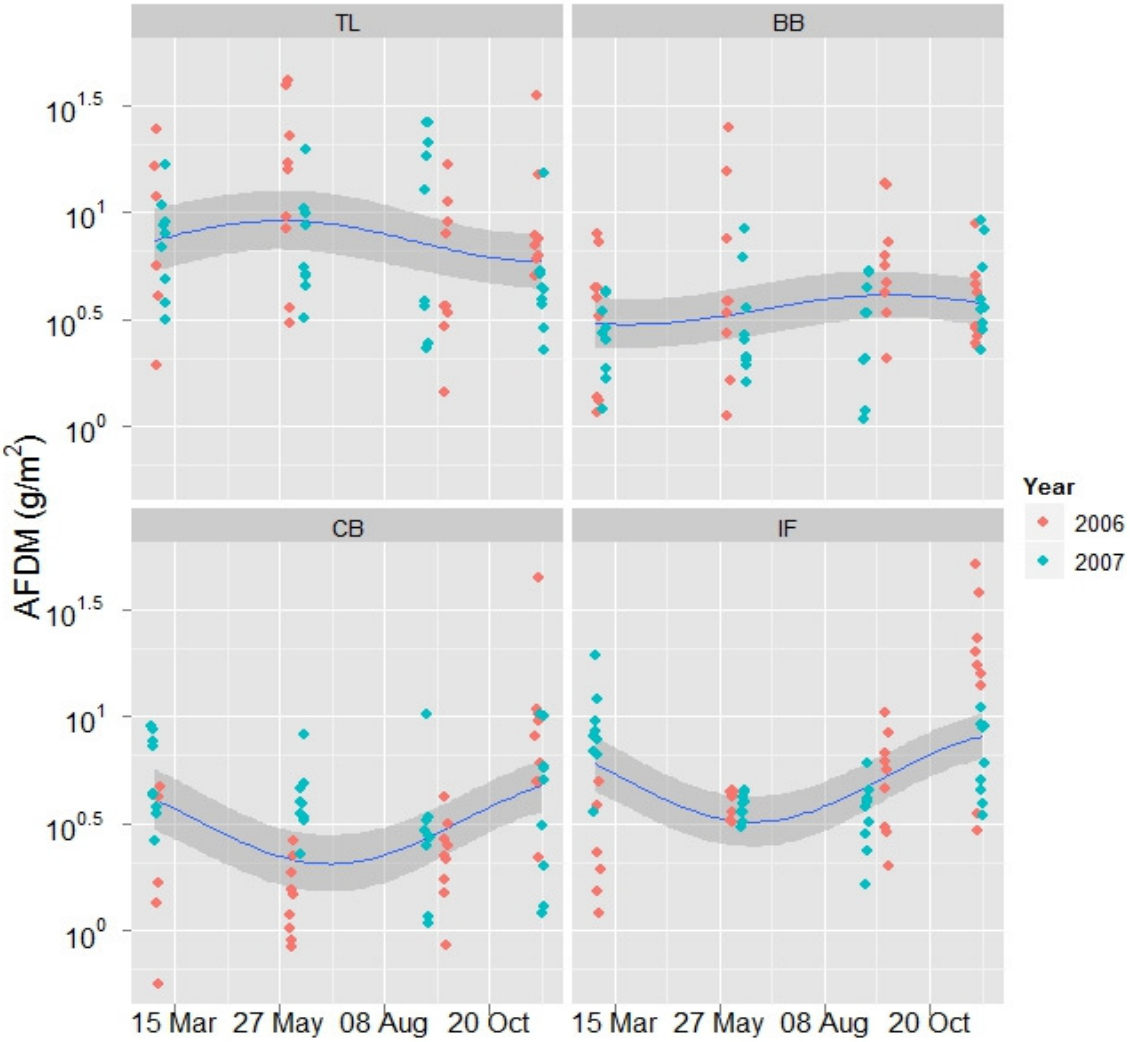


Fig. 4.1 Log_{10} biofilm mass ($g.m^2$) for all study sites. TL and BB represent the upstream and downstream sites on Tooms River, and CB and IF represent the upstream and downstream sites on Macquarie River, respectively. Red dots represent individual samples for 2006, blue dots are individual samples for 2007. The blue line shows the periodic regression trend over the 2 years, with 95% confidence intervals in grey.

Table 4.3 Parameter estimates from the periodic regressions of biofilm mass (AFDM) for each site with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the $\log_{10}$-tranformed scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the $\log_{10}$-transformed scale, and the "Date" is the date of this maximum value, which has been back-transformed from the phase angle values, θ, which are not shown here. The amplitude and date values shown in this table were not significant for the Tooms River sites, TL and BB.

Site	Mean	Arithmetic mean	Amplitude	Date
TL	0.867 (0.764, 0.969)	7.36 (5.81, 9.31)	0.259 (0.095, 0.302)	May 29 (Jul 27, Mar 05)
BB	0.546 (0.455, 0.636)	3.51 (2.85, 4.32)	0.186 (0.068, 0.290)	Sep 22 (Aug 22, Jan 29)
CB	0.502 (0.336, 0.668)	3.17 (2.17, 4.65)	0.336 (0.189, 0.569)	Dec 25 (Sep 09, Jan 29)
IF	0.699 (0.529, 0.869)	5.00 (3.38, 7.40)	0.397 (0.199, 0.552)	Dec 09 (Sep 11, Jan 25)

The very broad upper and lower limits of the amplitude and date for the Tooms River sites are due to the non-significant seasonality, so that the limits could be in either 2006 or 2007. This effect is also apparent in the periodic regression tables in the following data sections.

4.4.1.2 Chlorophyll a

Chlorophyll *a*, the autotrophic content of biofilms, had similar abundance trends to biofilms, with significantly higher levels at the regulated Tooms River sites (ANOVA, $F_{(3, 276)} = 5.569$, $p < 0.00001$). There was a highly significant seasonal variation at both the Macquarie sites, but no significant seasonal variation at the Tooms River sites (Table 4.4, Fig. 4.2).

Table 4.4 Significance of seasonal variation in chlorophyll *a* at each site. TL and BB are the upstream and downstream Tooms sites, and CB and IF are the upstream and downstream Macquarie sites, respectively.

Site	$F_{(1.63)}$	p
TL	2.33	0.105
BB	1.71	0.188
CB	10.30	< 0.001
IF	8.39	< 0.001

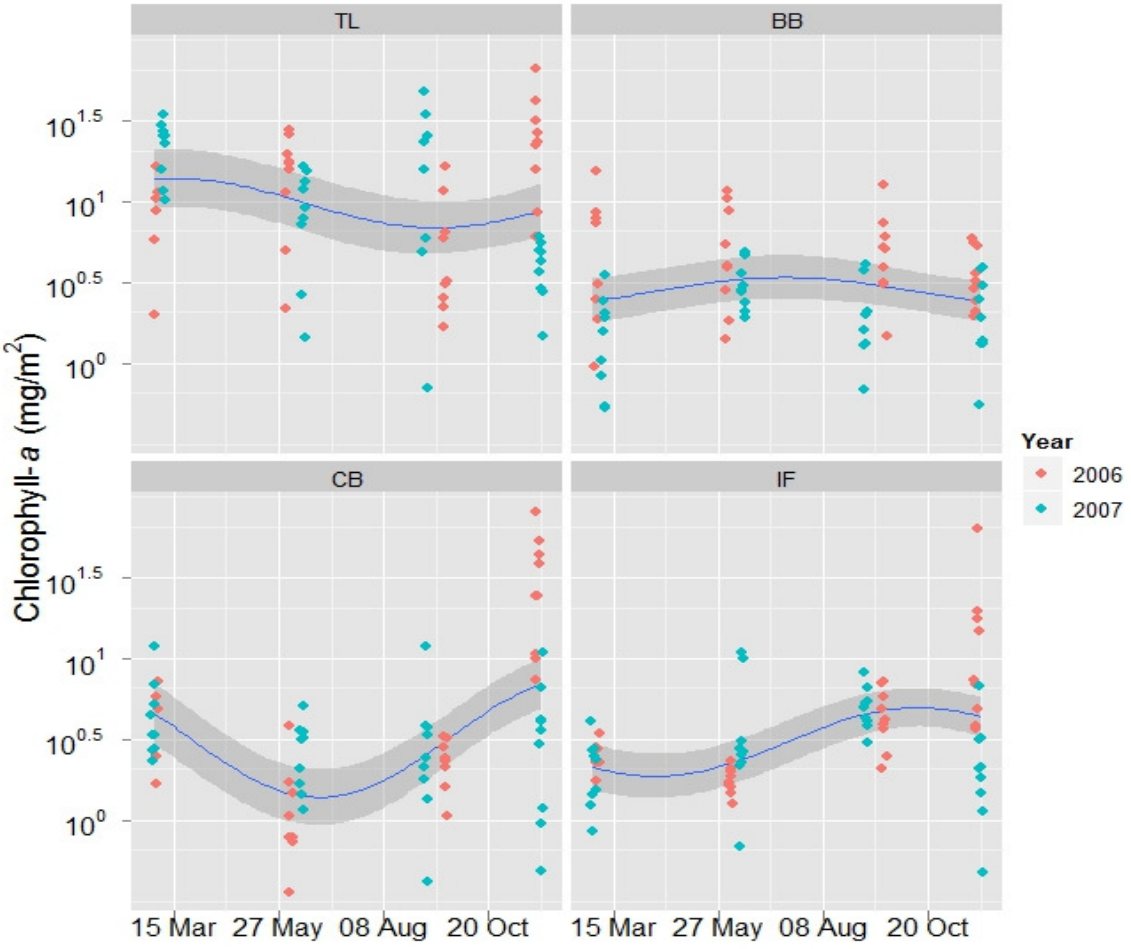


Fig. 4.2 Log_{10} chlorophyll *a* ($mg.m^2$) for all study sites. TL and BB represent the upstream and downstream sites on Tooms River, and CB and IF represent the upstream and downstream sites on Macquarie River, respectively. Red dots represent individual samples for 2006, blue dots are individual samples for 2007. The blue line shows the periodic regression trend over the 2 years, with 95% confidence intervals in grey.

Biofilm abundance at the Macquarie sites was usually higher at the downstream site, IF, but chlorophyll *a* abundance was often higher at the upstream site, indicating a higher degree of autotrophy at this site. Chlorophyll *a* was less abundant at the Macquarie sites in November 2007 than in November 2006.

Table 4.5 Parameter estimates from the periodic regressions of chlorophyll *a* for each site with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the $\log_{10}$-tranformed scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the $\log_{10}$-transformed scale, and the "Date" is the date of this maximum value, which has been back-transformed from the phase angle values, θ, which are not shown here. The amplitudes and date values shown in this table were not significant for the Tooms River sites, TL and BB.

Site	Mean	Arithmetic mean	Amplitude	Date
TL	0.996 (0.782, 1.210)	9.90 (6.06, 16.20)	0.440 (0.139, 0.676)	Mar 16 (Aug 04, Feb 18)
BB	0.446 (0.309, 0.582)	2.79 (2.04, 3.82)	0.246 (0.115, 0.465)	Jul 27 (Aug 09, Feb 20)
CB	0.498 (0.245, 0.752)	3.15 (1.76, 5.64)	0.584 (0.337, 0.859)	Dec 11 (Sep 15, Jan 23)
IF	0.508 (0.343, 0.674)	3.22 (2.20, 4.72)	0.368 (0.203, 0.556)	Oct 14 (Sep 02, Jan 15)

4.4.1.3 Autotrophic index

The autotrophic index (AI) indicates the degree of autotrophy or heterotrophy within the river. Algal dominated systems should have an AI of 50 -100 (Collins and Weber 1978). Almost all AI values in this study were less than 100 (Fig 4.3), indicating a high degree of autotrophy at all sites, with the highest AI values at the downstream Macquarie site, IF. There was a significant difference in the autotrophic indices between rivers ($F_{(3, 276)} = 2.964$, $p = 0.0326$), but no difference between sites on each river (all $p > 0.142$).

There was no seasonal variation in the AI at the downstream Tooms site, BB, but marginally significant seasonality at the upstream Tooms site, TL (Table 4.6). In contrast, while the two Macquarie sites were strongly seasonal, the highest levels of autotrophy at the upstream site, CB, were in early winter, yet occurred in autumn at the downstream site, IF (Fig. 4.3, Table 4.7)).

Table 4.6 Significance of seasonal variation in the autotrophic index for each site. TL and BB are the upstream and downstream Tooms sites, and CB and IF are the upstream and downstream Macquarie sites, respectively.

Site	$F_{(1, 63)}$	p
TL	2.780	0.069
BB	0.436	0.648
CB	10.100	< 0.001
IF	9.660	< 0.001

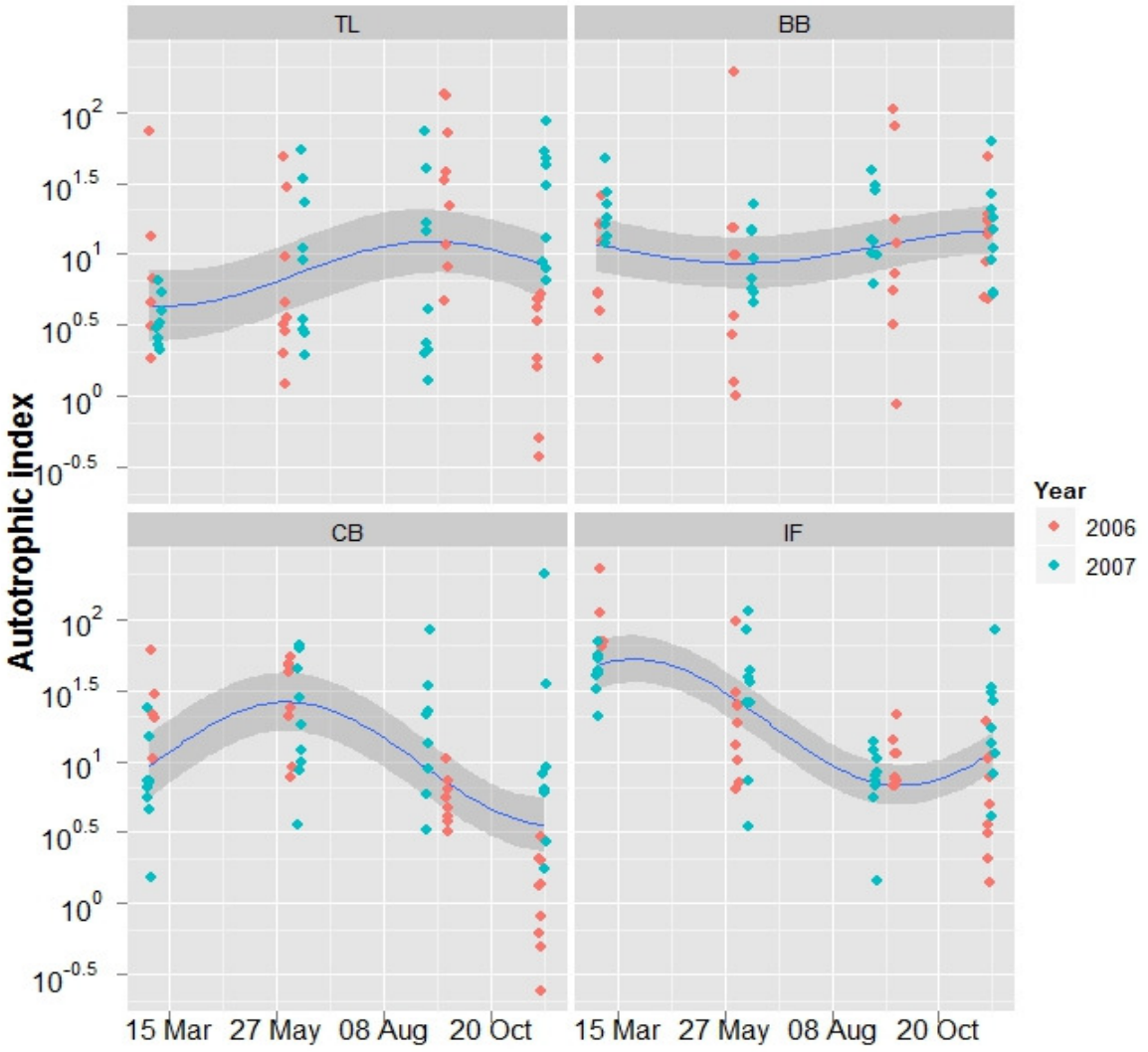


Fig. 4.3 Log_{10} autotrophic index for all study sites. TL and BB represent the upstream and downstream sites on Tooms River, and CB and IF represent the upstream and downstream sites on Macquarie River, respectively. Red dots represent individual samples for 2006, blue dots are individual samples for 2007. The blue line shows the periodic regression trend over the 2 years, with 95% confidence intervals in grey.

Table 4.7 Parameter estimates from the periodic regressions of the autotrophic index (AI) for each site with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the $\log_{10}$-tranformed scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the $\log_{10}$-transformed scale, and the "Date" is the date of this maximum value, which has been back-transformed from the phase angle values, θ, which are not shown here. The amplitude and date values shown here were non-significant for the Tooms River sites, TL and BB

Site	Mean	Arithmetic mean	Amplitude	Date
TL	0.881 (0.598, 1.160)	7.61 (3.97, 14.6)	0.551 (0.214, 0.928)	Sep 10 (Aug 20, Feb 02)
BB	0.946 (0.742, 1.150)	8.82 (5.52, 14.1)	0.515 (0.098, 0.559)	Nov 26 (Aug 24, Feb 02)
CB	0.942 (0.687, 1.200)	8.74 (4.86, 15.7)	0.653 (0.431, 0.898)	Jun 04 (Jul 18, Mar 24)
IF	1.230 (1.090, 1.370)	17.1 (12.3, 23.7)	0.355 (0.278, 0.665)	Mar 31 (Jun 10, Mar 08)

4.4.2 Vascular macrophytes

The downstream Macquarie site IF, had the greatest diversity of macrophytes (Fig.4.4). *Triglochin procerum* R. Br. and *Myriophyllum salsugineum* Orchard were abundant at this site, and *Potamogeton tricarinatus* F. Muell & A. Benn and several minor species were common in the study reach, with abundant *Juncus* sp. and *Eleocharis* sp. fringing deeper pools. *Juncus* and *Eleocharis* were moderately abundant at the upstream Macquarie site, CB, but fully aquatic macrophyte species were restricted to *M. salsugineum,* which dominated most pools, and occasional *T. procerum* plants in a few pools.

Fig 4.4 Macrophyte beds in a shallow pool at the downstream Macquarie site, IF, in November 2007. The inset photo is of *Triglochin procerum* in a deeper pool at the same site.

In contrast, *Eleocharis* was not observed at the Tooms sites, although *Juncus* was moderately abundant on the banks at the downstream site, BB. Sparse growth of *Triglochin procerum* was observed at this site on rare occasions, but there was prolific growth of *Potamogeton tricarinatus* in an artificial pool above a low weir, below the study reach (Fig. 4.5). Charophytes were common at both Tooms sites, but did not occur at the Macquarie sites. Vascular macrophytes were not observed at the upstream Tooms site, TL, although *T. procerum* was moderately abundant in the lake littoral zone and in the pool upstream of the gauging weir.

Fig. 4.5 *Potamogeton tricarinatus* (top inset) at the downstream Tooms site, BB, in July 2007, above a low rock weir. The lower photo is an enlargement of the unidentified brown mucilage, probably the cyanobacterium *Synechocystis* sp., with the lower inset showing the same mucilage at 1000x magnification and with differential interference.

4.4.3 Total suspended solids

The highly turbid water noted in Tooms River was due to organic material, rather than suspended inorganic sediments. Suspended organic material, measured as total suspended solids, was significantly higher in Tooms River ($F_{(1, 24)} = 24.156$, $p = 0.00005$) (Fig.4.6). All sites had similar concentrations in November 2006, when suspended organic material began to increase in Tooms River, peaking in late summer and decreasing again in winter 2007. Suspended OM was generally higher at TL, near the lake, followed closely by BB. This dropped to baseline levels at BB in winter 2007 with input from minor tributaries after heavy rain, before increasing again to match TL.

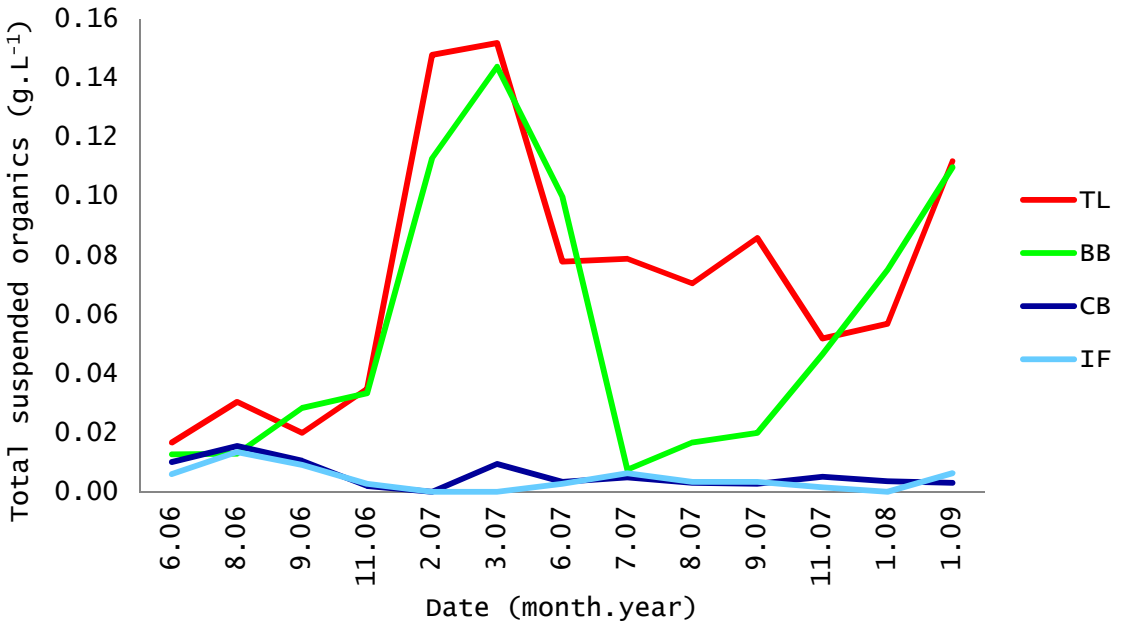


Fig.4.6. Total suspended organic material (g.L^{-1}) for each sample date, where TL and BB are the upstream and downstream Tooms sites, and CB and IF are the upstream and downstream Macquarie sites, respectively. The trends of the individual sites are indicated by the colours shown in the key.

4.4.4 Nutrient concentrations

Total dissolved nitrogen, phosphorus and total organic carbon concentrations were all significantly higher in Tooms River than in the Macquarie River (Table 4.8). There was no significant difference between

upstream and downstream sites on each river (two-tailed Students *t*-test, Tooms $p = 0.266$, Macquarie $p = 0.858$), but all nutrients had higher concentrations at TL than at BB.

Table 4.8 Significant differences between the regulated Tooms River and unregulated Macquarie River for total dissolved nitrogen and phosphorus and total organic carbon concentrations in water samples (milligrams per litre), showing the mean values ($\bar{x}$) ± 1 standard deviation, with the number of samples (*n*) in parentheses.

Variable (mg.L^{-1})	Tooms $\bar{x}$ (n = 26)	Macquarie $\bar{x}$ (n = 22)	F	p
Nitrogen	0.47 ± 0.130	0.28 ± 0.131	9.958	0.0049
Phosphorus	0.017 ± 0.005	0.007 ± 0.002	24.967	< 0.0001
Carbon	17.13 ± 5.390	6.75 ± 2.195	24.629	< 0.0001

4.4.5 Allochthonous resources

4.4.5.2 Leaf buoyancy

All leaves sank more rapidly in moving water than in still or slowly moving water, with *E. viminalis* sinking faster than the other species (upper panel, Fig. 4.7). However, there was no significant difference in median flotation time (D_{50}) between the largest leaves, *E. viminalis*, and the smallest leaves, *Leptospermum lanigerum*. *Eucalyptus pulchella* and *A. mucronata* also had similar median flotation times to each other, although *E. pulchella* was most buoyant overall. In slowly moving water, the two eucalypt species had the fastest sinking leaves. Initially *E. pulchella* leaves sank more rapidly than the other species, but a few leaves remained floating for an extended time (lower panel, Fig. 4.7). *Leptospermum lanigerum* had a significantly higher median flotation time than the other three species (Table 4.9).

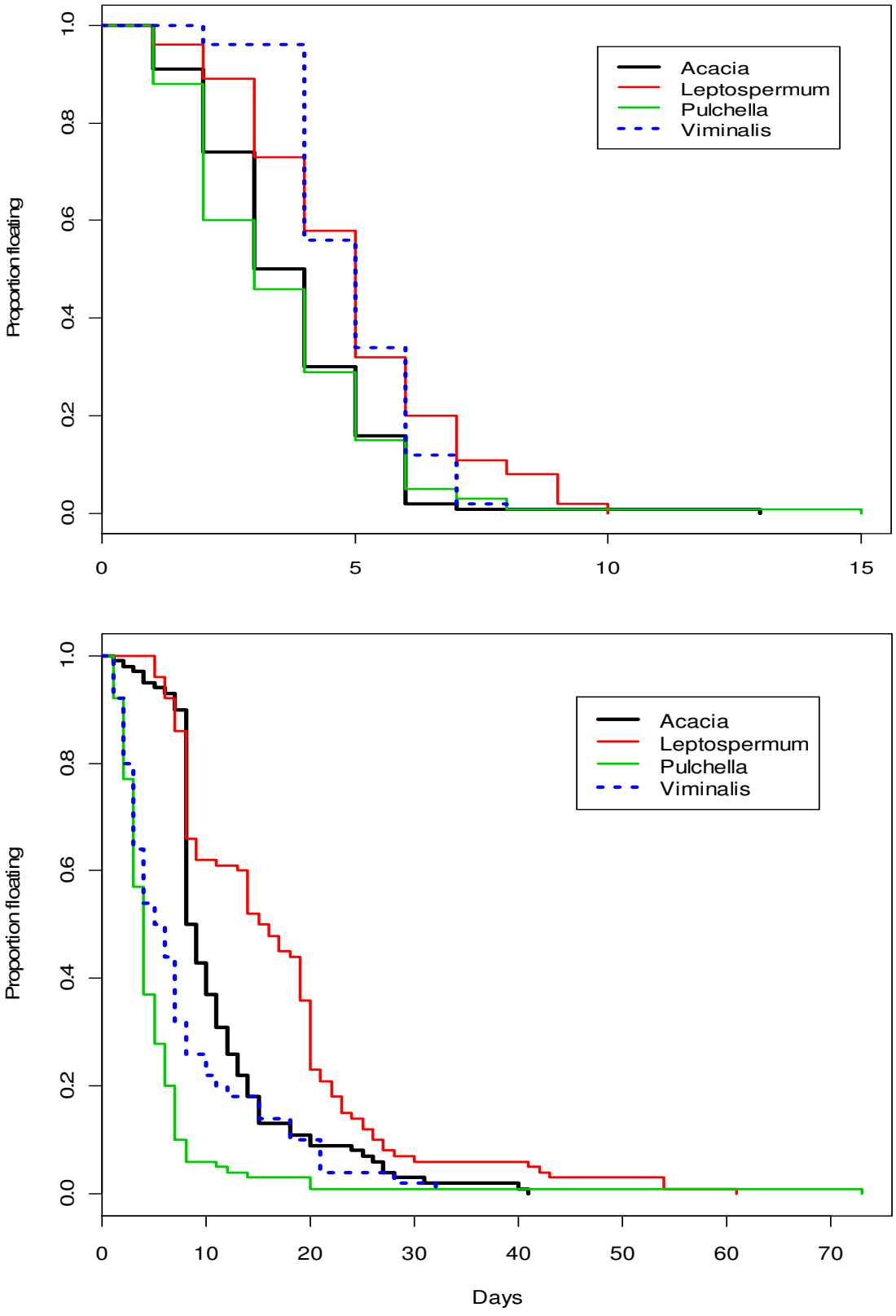


Fig. 4.7 Mean proportion of leaves remaining afloat in moderately fast moving water (upper panel) and in slowly moving water (lower panel), for each leaf species with time (days) on the *x*-axis. Different scales are used on the x-axes (Days) of each panel.

Table 4.9 Median flotation times (D_{50}) in days for each leaf type, in slow flow and moderately fast flowing water.

Leaf species	Slow flow D_{50}	Moderate flow D_{50}
Acacia mucronata	8.5	3.5
Eucalyptus pulchella	4.0	3.0
Eucalyptus viminalis	5.5	5.0
Leptospermum lanigerum	16.0	5.0

In completely still water, a few leaves sank in the first few days, but most leaves were still floating at 100 days, when the trial was abandoned. *Eucalyptus pulchella* initially sank faster than the other leaves, but *E. viminalis* leaves began to decompose at about day 90. The low number of leaves sinking in still water prevented calculation of a median flotation time for this flow rate. However, the difference between the recorded flotation times of the leaf species in still water was insignificant (X^2, p = 0.398).

4.4.5.1 Benthic organic material

Benthic leaf litter was patchily distributed at all sites, but abundance generally correlated with times of highest flow - in summer in Tooms River and in winter or spring in the Macquarie. Table 4.10 shows that there was no seasonal variation in BOM at the upstream Macquarie site, CB, but significant seasonal variation at both the Tooms sites and at the downstream Macquarie sites.

Table 4.10 Significance of seasonal variation in total benthic organic material for each site. TL and BB are the upstream and downstream Tooms sites and CB and IF are the upstream and downstream Macquarie sites, respectively.

Site	$F_{(1, 80)}$	p
TL	5.820	0.004
BB	4.190	0.019
CB	0.507	0.604
IF	5.550	0.006

Tooms River had significantly more total litter, leafy detritus and woody material than the unregulated Macquarie River ($p < 0.05$), but the degree of difference varied between collection rounds (Fig.4.8, Table 4.11).

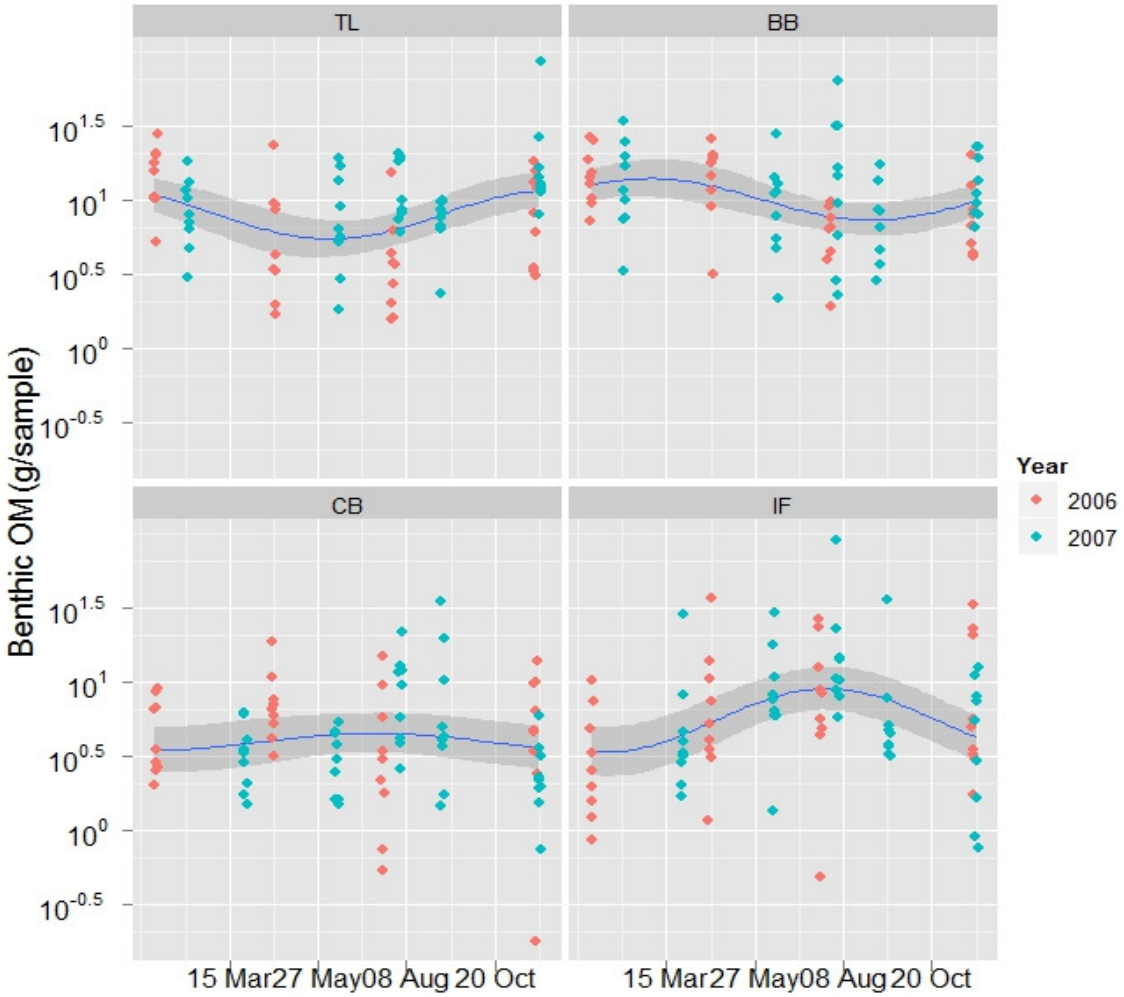


Fig. 4.8 Log_{10} benthic organic matter mass (g) for all study sites. TL and BB represent the upstream and downstream sites on Tooms River, respectively. CB and IF represent the upstream and downstream sites on Macquarie River, respectively. Red dots represent individual samples for 2006, blue dots are individual samples for 2007. The blue line shows the periodic regression trend over the 2 years, with 95% confidence intervals in grey.

Table 4.11 Parameter estimates from the periodic regressions of benthic organic litter mass for each site with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the $\log_{10}$-tranformed scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the $\log_{10}$-transformed scale, and the "Date" is the date of this maximum value, which has been back-transformed from the phase angle values, θ, which are not shown here. The amplitude and date values shown here were non-significant for the upstream Macquarie site, CB.

Site	Mean	Arithmetic mean	Amplitude	Date
TL	0.903 (0.773, 1.030)	8.00 (5.93, 10.80)	0.338 (0.164, 0.395)	Dec 05 (Sep 22, Jan 29)
BB	1.010 (0.925, 1.090)	10.20 (8.40, 12.40)	0.140 (0.074, 0.351)	Mar 01 (Feb 25, Aug 12)
CB	0.601 (0.462, 0.740)	3.99 (2.90, 5.49)	0.298 (0.058, 0.388)	Jul 12 (Feb 25, Aug 15)
IF	0.744 (0.650, 0.838)	5.55 (4.47, 6.89)	0.214 (0.101, 0.434)	Jul 24 (Apr 27, Aug 07)

Eucalyptus, Acacia and *Leptospermum* were the most abundant leaves in the benthos. SIMPER analysis showed that *Acacia* and eucalypt leaves were more abundant in Tooms River than in the Macquarie River, while *Leptospermum* leaves were more abundant in the Macquarie River (Table 4.12). There were also differences between the sites within each river (Table 4.13). *Acacia* phyllodes were the most abundant 'leaf' at every site, with eucalypt leaves more important than *Leptospermum* leaves at all sites except the downstream Macquarie site, IF, where grass blades made a contribution. *Pomaderris apetala* (Rhamnaceae) leaves were also common in benthic samples from the downstream Tooms site, BB.

Table 4.12 SIMPER average abundance scores between rivers for the main benthic leaf species, showing the average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that species to the similarity, and cumulative percentage to the total abundance

Species	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Tooms River: Average similarity between samples: 71.45					
Acacia	1.46	22.48	3.03	31.46	31.46
Eucalyptus	1.46	21.11	2.80	29.55	61.01
Leptospermum	0.97	13.87	1.99	19.41	80.42
Other	0.76	8.97	1.09	12.56	92.98
Macquarie River: Average similarity between samples: 65.71					
Acacia	1.39	20.87	2.80	31.77	31.77
Leptospermum	1.10	16.21	2.76	24.67	56.44
Eucalyptus	1.26	15.15	1.43	23.06	79.49
Other	0.73	7.24	0.90	11.01	90.51

Table 4.13 SIMPER average abundance scores between sites for the main benthic leaf species, showing the average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that species to the similarity, and cumulative percentage to the total abundance

Species	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Upstream Tooms River site, TL: Average similarity between samples: 75.94					
Acacia	1.50	25.98	4.29	34.21	34.21
Eucalyptus	1.48	23.63	3.21	31.12	65.34
Leptospermum	0.94	13.81	1.63	18.18	83.52
Other	0.81	11.36	1.31	14.96	98.48
Downstream Tooms River site, BB: Average similarity between samples: 72.22					
Acacia	1.41	19.30	2.53	26.73	26.73
Eucalyptus	1.44	18.79	2.59	26.02	52.75
Leptospermum	1.00	13.96	2.70	19.34	72.09
Pomaderris	0.95	10.21	1.35	14.13	86.22
Other	0.71	6.87	0.94	9.51	95.73
Upstream Macquarie River site, CB; Average similarity between samples: 68.35					
Acacia	1.37	21.51	2.58	31.47	31.47
Eucalyptus	1.48	20.35	1.85	29.77	61.24
Leptospermum	1.03	15.62	2.32	22.85	84.09
Other	0.65	6.00	0.74	8.78	92.87
Downstream Macquarie River site, IF; Average similarity between samples: 66.87					
Acacia	1.42	20.24	3.10	30.26	30.26
Leptospermum	1.17	16.85	3.51	25.20	55.46
Eucalyptus	1.04	11.05	1.20	16.52	71.99
Other	0.80	8.53	1.11	12.76	84.75
Grass	0.60	4.51	0.63	6.75	91.50

Similarity between samples was lower at the Macquarie sites for both leafy and woody litter components. The woody components of benthic litter mass were most abundant at times of high flow, in winter and spring at the Macquarie sites, and in summer at the Tooms sites. Twigs and bark were the most abundant woody components at all sites, forming 61% and 68% of the total woody litter in the regulated Tooms and unregulated Macquarie Rivers, respectively. Eucalypt fruit formed an additional 15.8% of the woody litter in Tooms River, but were less than 4% of woody litter in the Macquarie. There was also variation in the abundance of woody litter between sites within rivers (Table 4.14).

Acacia fruit were only abundant at the two downstream sites. Wood contributed 8% to the similarity between samples at the Macquarie sites, but was not important at the Tooms sites. In contrast, eucalypt fruit capsules were more abundant at the Tooms River sites, and least abundant at IF. Leptospermum seed capsules were most abundant at all sites at times of highest flow, with peak abundance at both Macquarie sites with the spring 2007 spate.

Table 4.14 SIMPER average abundances (grams) between sites for the main woody components of the benthic litter, showing the average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that species to the similarity, and cumulative percentage to the total abundance

Species	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Upstream Tooms River site, TL: Average similarity between samples: 53.31					
Twigs	0.98	24.04	2.10	45.09	45.09
Eucalyptus fruit	0.56	11.21	1.10	21.03	66.12
Bark	0.42	8.30	1.27	15.57	81.69
Leptospermum frt	0.27	6.90	1.27	12.94	94.63
Downstream Tooms River site, BB: Average similarity between samples: 58.05					
Twigs	0.96	19.58	2.37	33.73	33.73
Bark	0.85	15.29	1.71	26.34	60.07
Acacia fruit	0.32	7.06	1.67	12.17	72.24
Eucalyptus fruit	0.34	6.60	1.33	11.36	83.60
Leptospermum frt	0.27	6.06	1.60	10.44	94.05
Upstream Macquarie River site, CB; Average similarity between samples: 49.93					
Twigs	0.71	20.90	1.79	41.86	41.86
Bark	0.57	13.57	1.34	27.17	69.03
Leptospermum frt	0.27	6.74	1.07	13.51	82.54
Wood	0.31	4.02	0.62	8.05	90.59
Downstream Macquarie River site, IF; Average similarity between samples: 42.14					
Twigs	0.73	17.96	1.51	42.62	42.62
Bark	0.42	9.37	1.02	22.23	64.85
Acacia fruit	0.21	5.77	0.85	13.70	78.56
Leptospermum frt	0.18	4.56	0.87	10.83	89.38
Wood	0.41	3.41	0.47	8.10	97.48

4.4.5.3 Benthic cellulose decomposition potential

Mean benthic cellulose tensile strength loss was significantly higher, but more variable at TL for both treatment types (ANOVA - coarse mesh $F_{(1, 18)} = 26.679$, $p < 0.001$; fine mesh $F_{(1, 18)} = 20.978$, $p < 0.001$). Mean cellulose tensile strength loss (CTSL) was lower at the Macquarie sites than at the downstream Tooms site BB for both treatments, although this was not significantly different. Mean CTSL was significantly higher in coarse mesh bags (upper panel Fig. 4.9), where strips were exposed to invertebrate feeding activity than in fine mesh bags for all sites except the downstream Tooms site, BB (lower panel, Fig. 4.9, Table 4.15).

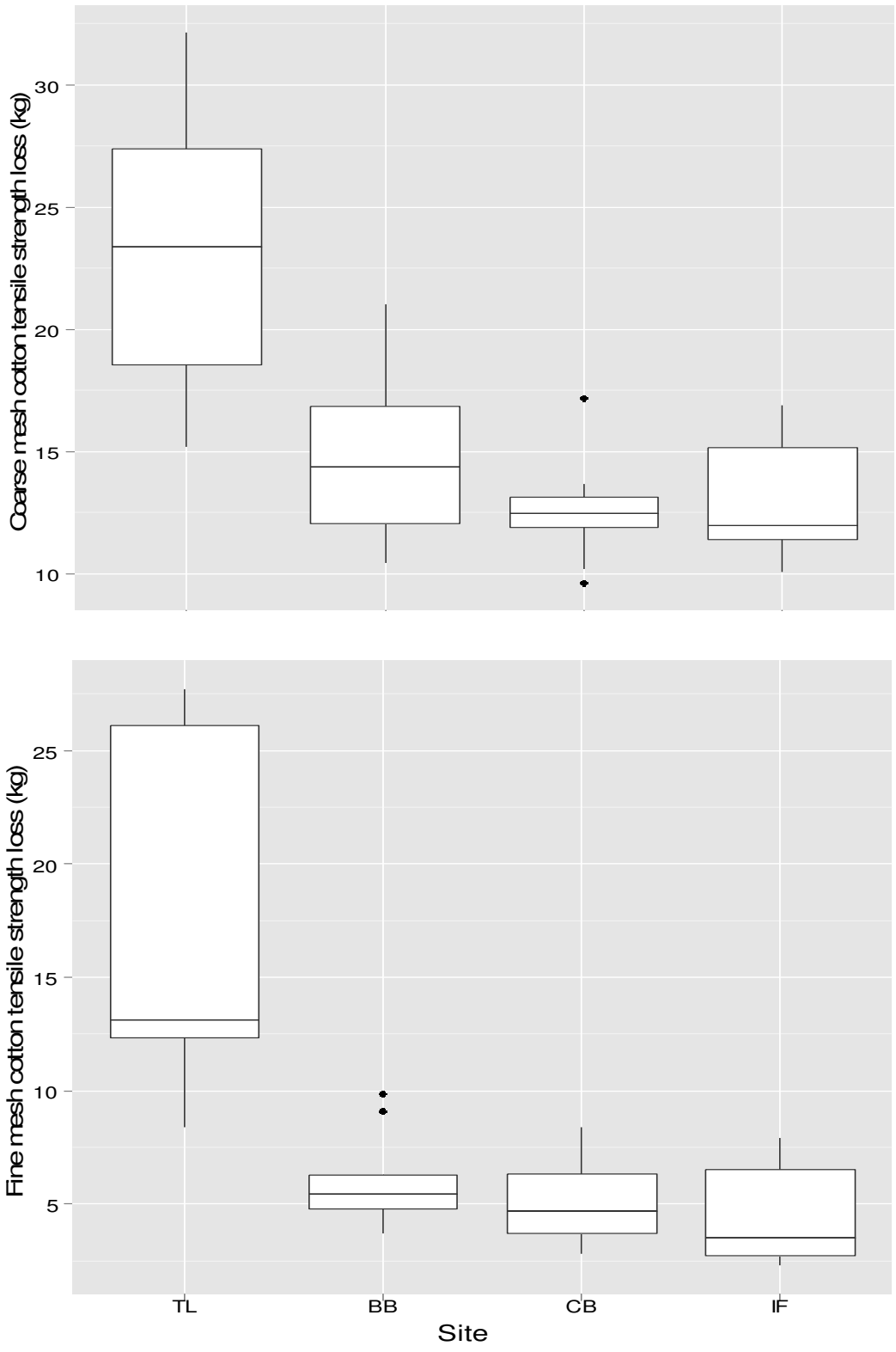


Fig. 4.9 Box plots (mean and standard deviation) of tensile strength loss (kg) of benthic cotton strips in coarse mesh bags (upper panel) and fine mesh bags (lower panel). TL and BB are the upstream and downstream Tooms sites; CB and IF are the upstream and downstream Macquarie sites, respectively.

Table 4.15 Two-tailed *t*-test comparisons between benthic coarse mesh and fine mesh cotton strip tensile strength loss. TL and BB are the upstream and downstream Tooms sites, and CB and IF are the upstream and downstream Macquarie sites, respectively.

Site	*t*-stat	*p*
TL	-1.9151	< 0.0001
BB	-6.5049	0.0725
CB	-7.9537	< 0.0001
IF	-8.3390	< 0.0001

4.4.5.4 Benthic leaf decomposition

Cellulose decomposition potential indicated higher decomposition rates at the Tooms River sites. In support of this, benthic leaf litter was also more decomposed at these sites. The greatest seasonal variation in leaf decomposition was at TL and IF (Table 4.16), with leaves collected in winter the most fragmented at all sites (Fig. 4.10, Table 4.17). There was no significant seasonality of litter decomposition at either BB or CB.

Table 4.16 Significance of seasonal variation in decomposition of benthic organic material for each site. TL and BB are the upstream and downstream Tooms sites, and CB and IF are the upstream and downstream Macquarie sites, respectively.

Site	$F_{(1, 80)}$	*p*
TL	5.10	0.008
BB	1.87	0.162
CB	0.36	0.699
IF	3.26	0.044

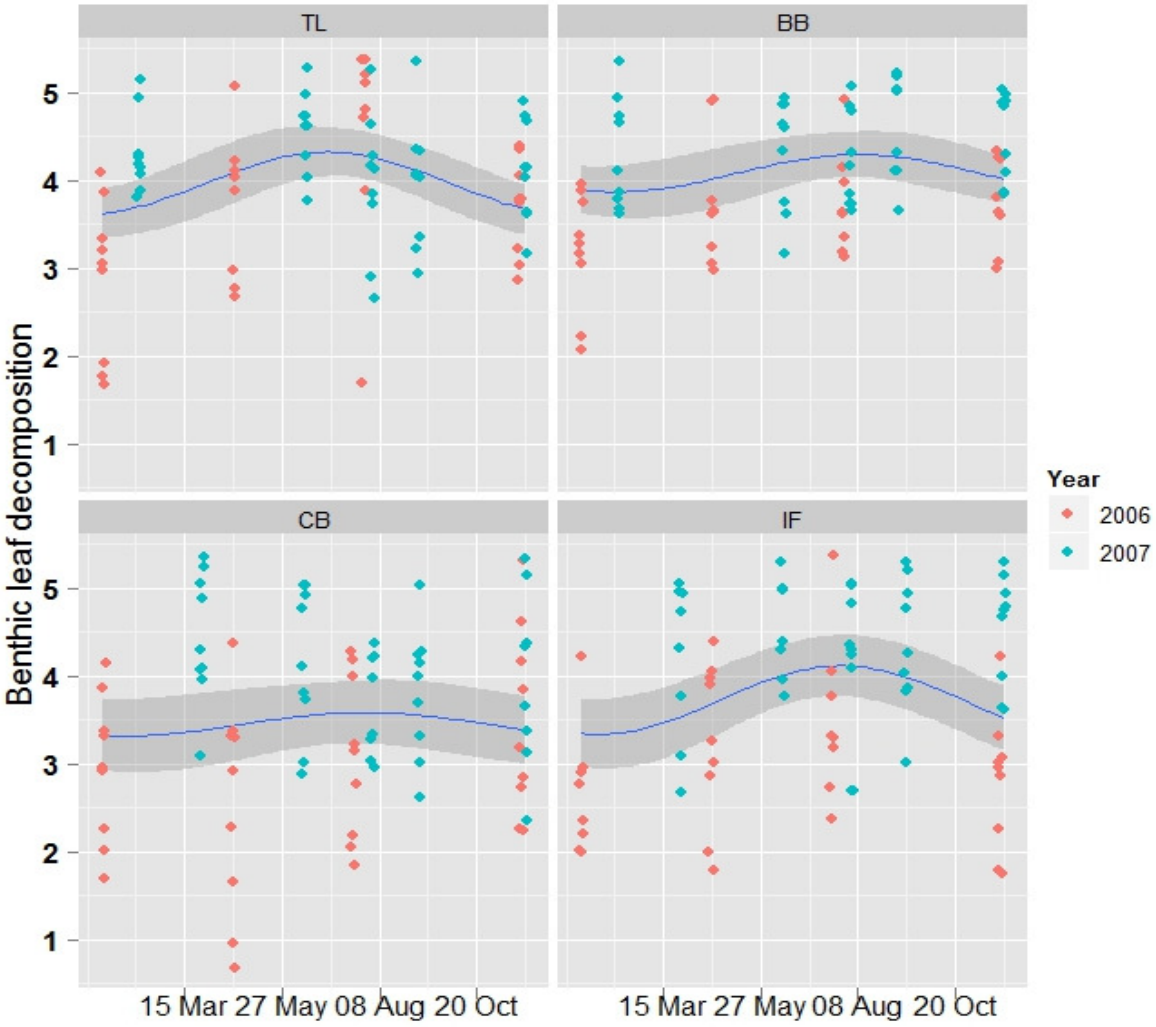


Fig. 4.10 Benthic leaf decomposition for all study sites, on an ordinal scale, where a larger number indicates greater decomposition. TL and BB represent the upstream and downstream sites on Tooms River, respectively, CB and IF represent the upstream and downstream sites on Macquarie River, respectively. Red dots represent individual samples for 2006, blue dots are individual samples for 2007. The blue line shows the periodic regression trend for the 2 years, with 95% confidence intervals in grey.

Table 4.17 Parameter estimates from the periodic regressions of benthic leaf litter decomposition for each site with 95% confidence intervals given in parentheses. "Mean" refers to the average mass (or mesor) on the ordinal scale, and values have been back-transformed in the column labelled "Arithmetic mean". "Amplitude" is the maximum value above the mean on the ordinal scale, and the "Date" is the date of this maximum value, which has been back-transformed from the phase angle values, θ, which are not shown here. The amplitude and date values shown here were non-significant for the upstream Macquarie site, CB and the downstream Tooms site, BB.

Site	Mean	Arithmetic mean	Amplitude	Date
TL	0.588 (0.546, 0.631)	3.88 (3.51, 4.28)	0.0894 (0.0405, 0.1360)	Jul 01 (Mar 16, Aug 10)
BB	0.602 (0.561, 0.643)	4.00 (3.64, 4.40)	0.0777 (0.0268, 0.1300)	Aug 09 (Feb 28, Aug 21)
CB	0.515 (0.448, 0.583)	3.28 (2.80, 3.83)	0.1380 (0.0285, 0.1950)	Aug 20 (Feb 18, Aug 22)
IF	0.554 (0.485, 0.622)	3.58 (3.05, 4.19)	0.1240 (0.0533, 0.2180)	Jul 24 (Mar 01, Aug 13)

4.5 Discussion

Contrary to the predictions of Table 4.1, the low light levels in Tooms River did not suppress the biomass of photosynthetic algae, which were more abundant at these sites than in the Macquarie River. In contrast to the regulated sites, where there was no seasonal variation in biofilm abundance, the variable flow regime in the Macquarie River influenced biofilm abundance, with peak abundance in summer when the river was reduced to pools, and lowest abundance with winter and spring spates, as was also reported by Biggs (1989) and Rounick and Gregory (1981).

As expected (Table 4.1), benthic litter abundance was higher at the Tooms River sites, but peak abundance was out of phase between the regulated and unregulated rivers. In contrast to biofilm abundance, which occurred at times of lowest flow, maximum benthic litter abundance coincided with periods of highest flow - in winter in the Macquarie River, and in summer in Tooms River.

4.5.1 Autochthonous resources

Biofilms were expected to be more abundant at the upstream Tooms site, TL, but the high chlorophyll *a* levels at this site (Fig. 4.2) were surprising, because the overhanging riparian canopy and high turbidity were predicted to suppress autotrophy in Tooms River (cf. Lock *et al.* 1984). The autotrophic index (Fig. 4.3) indicated algal dominated systems in both rivers, although the abundance of organic detritus (Fig. 4.9) and high DOC levels (Table 4.7) in Tooms River were expected to stimulate heterotrophic fungal and bacterial productivity (Artigas *et al.* 2009). Unexpectedly, the highest autotrophic indices were at the downstream Macquarie site, IF, the site with the highest light levels. Higher AI usually indicates a trend towards an heterotrophic system (Collins and Weber 1978). It is possible that the shallow pools which developed in summer at IF were warm enough to favour bacteria or fungi rather than green algae.

The majority of studies of regulated streams are of deep-release reservoirs (e.g. Dufford *et al.* 1985). In most cases, the result of impoundment is an increase in algal biomass, particularly proliferation of filamentous green algae below the dam (e.g. Sheldon and Walker 1997), leading to high chlorophyll *a* levels in the benthic biofilms, stimulated by the release of nutrient-rich bottom water from reservoirs (Neel 1963). Nichols *et al.* (2006) found biofilms rather than filamentous algae below two dams on the Cotter River in the Australian Capital Territory, but filamentous algae dominated below the third and least regulated dam. Green filamentous algae were not found in Tooms River, and were only found at the unregulated Macquarie sites.

Diatoms dominated biofilms at the lower Tooms site, BB. The spring peak in chlorophyll *a* at this site was probably due to the prolific diatom growth observed at this site (Fig.4.11), because diatoms contain chlorophyll *a*, in combination with chlorophyll *c* (Ritchie 2006). Diatoms dominated below six dams in central Portugal (Caramujo *et al.* 2008),

increasing in abundance with low flows under drought conditions. Eutrophic conditions stimulated a spring diatom bloom in the Murray-Darling River system in Australia (Walker 1979), while Lawson and Rushforth (1975) showed that high nutrient levels stimulated growth of the diatom *Cymbella prostrata* below dams on the Provo River in Utah. This species is considered an indicator of eutrophic conditions (Lowe 1974; ,cited in Lowe 1979). It is possible that the *Cymbella* sp. blooms observed in Tooms River are due to a flush of nutrients with increased stream flow in spring. However, there are many *Cymbella* species, found across a broad range of environmental conditions (Tornés *et al.* 2007). Diatoms were also found in the Macquarie River, but thick biofilm mats are unlikely to develop in the more variable flow regime, where low profile growth forms would be more common (Peterson 1996).

Fig. 4.11 Stalked *Cymbella* sp. diatom bloom at BB in September 2006.

High chlorophyll *a* concentrations can also be produced in light-limited algae in thick biofilms, which may increase their concentration of photosynthetic pigments to maximise light sequestration (Hudon *et al.* 1987). Despite this, Tuchman (1996) suggested that some algae in low light environments were able to assimilate enough carbon from DOC to

reduce their dependence on photosynthesis. Furthermore, positive feedback can develop, where high DOC concentrations stimulate photosynthetic algal biomass (Meyer *et al.* 1998). Exudates from the biofilms lead to increased DOC levels (Kaplan and Bott 1982), further stimulating algal biomass. Increased heterotrophic biofilm activity has also been documented in DOC- and phosphorus-enriched streams (Ardon and Pringle 2007). It is clear that further intensive studies are needed to clarify the pathways of carbon use which might be responsible for biofilm communities in Tooms River.

Because biofilms obtain nutrients from the substrate and the water column (Suberkropp 1998), their abundance has been linked to nitrogen and phosphorus enrichment (Rosemond *et al.* 1993). Nutrient levels were significantly higher in Tooms River than in the Macquarie and were considerably higher than total nitrogen and total phosphorus levels in the regulated Cotter River in the Australian Capital Territory (Nichols *et al.* 2006). Nitrogen and phosphorus concentrations in the Macquarie River in contrast, were lower than those recorded in unregulated tributaries of the Cotter River (Nichols *et al.* 2006).

Maltby (1988) showed that cotton strips decomposed more rapidly in water with high nitrogen and phosphorus loads, while Young (2006) found a positive correlation between cellulose strip strength loss and inorganic nitrogen concentration, although bacteria from treated sewage effluent influenced his results. Nitrogen concentrations could partially explain the greater cellulose strength loss in Tooms River.

Although Croome and Tyler (1973, 1975) classified Tooms Lake as oligotrophic, cyanobacterial blooms (*Synechocystis* sp.) were reported with low lake levels in 2006 (SOER 2009). Cautionary government warning signs were posted on the lake shore for most of the study period. Low flows also produced high cyanobacteria levels in dams of the Murray-Darling River system (Baldwin *et al.* 2009). Cyanobacteria could

have contributed to the high chlorophyll *a* levels in Tooms River, because chlorophyll *a* is the main photosynthesising pigment in cyanobacteria (e.g. Ritchie 2006). Some cyanobacteria have been shown to prefer low light conditions (Ritchie 2006), as are found in Tooms River, although the high chlorophyll *a* levels at the upstream Tooms River site may have been enhanced by movement of cyanobacteria from Tooms Lake.

It is possible that the high abundance of cyanobacteria observed at the Tooms River sites is partially due to invertebrates selectively feeding on other biofilm types (Steinman 1996). Several studies have shown that invertebrate feeding activity can influence biofilm abundance and species composition (e.g. Steinman *et al.* 1987; Feminella *et al.* 1989; Hill *et al.* 1995). Grazing invertebrates in low nutrient streams reduced biofilm abundance (Biggs 2000), while snails limited green algal growth in experimental channels (Hill *et al.* 1995). However, although Rosemond (1993; 1993) showed that invertebrates selected diatoms in preference to cyanobacteria, stable isotope analyses indicated that cyanobacteria were an important component of Tooms River invertebrate diets (Chapter 6.1).

Invertebrate feeding activity can also influence litter decomposition rates, as indicated by the greater cellulose tensile strength loss in coarse mesh bags at all sites. While CTSL was significantly higher at TL than the other sites, this correlated with the higher abundance of collector-gatherers at this site (Chapter 5). Young (2006) asserted that invertebrates were unlikely to consume cotton strips, but Clapcott (2007) found sporadic substantial amphipod feeding activity on cotton strips in small Tasmanian streams. Ceinidae (Amphipoda), the most likely consumer, were abundant at all sites except the downstream Tooms site, BB, which may explain the non-significant effect of mesh size on CTSL at this site. Amphipods and other less common shredders are likely to have accelerated tensile strength loss in coarse mesh bags at the other 3 sites.

Stream temperature affects microbial activity and thus alters decomposition rates (Young *et al.* 2004), and is a major factor in most studies where hypolimnial water is released from deep reservoirs (e.g. Petts 1984). This is unlikely to be a factor in this study, because the temperature difference between rivers and between sites within rivers was non-significant (Table 4.1). Tooms Lake is shallow and does not stratify (Croome and Tyler 1972), so even though bottom water is released to the river, this is not significantly colder than the surface water.

However, the periods of zero flow in the Macquarie River are likely to have slowed cellulose and leaf litter decomposition at the Macquarie sites. Anderson *et al.* (2003) found that dry *Populus deltoides* leaves decomposed more slowly than leaves in the benthos of a Colorado river. Baldwin and Mitchell (2000) suggested that microbial activity would decrease as sediments dried, but that there would be a pulse of inorganic nitrogen and phosphorus as these sediments were rewetted, which would stimulate macrophyte and bacterial productivity.

Some vascular macrophyte species are recognised as increasing in abundance downstream of impoundments. For example, Décamps *et al.* (1979) recorded an increase in the abundance of *Potamogeton crispus* below dams on the Dordogne and Truyère Rivers in France, which they attributed to the reduction in high flows. *Potamogeton tricarinatus* was only observed in pools at the two downstream sites. This species was absent from fast flowing river sections and from both upstream sites.

4.5.2 Allochthonous resources

Benthic leaf mass was highest at all sites after heavy rain in August 2007, although this was not accompanied by overbank flows in Tooms River. This is in direct contrast to Boulton and Lake (1992a), who found that BOM was highest at times of zero flow in two south-eastern Australian intermittent streams. However, the greatest seasonal

variation in benthic litter abundance was at the downstream Macquarie River site (IF) which completely dried out in summer.

The abundance of the dominant leaf species in the benthos was influenced by the buoyancy of individual leaf types, the flow regime during the study period, and by long–term changes to the riparian vegetation. Mean annual benthic litter mass was lowest at the upstream Macquarie site, CB, (63.67 $g.m^{-2}$) and highest at the downstream Tooms site, BB (131.31 $g.m^{-2}$), although this was low by Australian standards. Most Australian studies of benthic litter deposition have been in flow-dependent river red gum (*Eucalyptus camaldulensis*) forests of the Murray-Darling River system (Thomas *et al.* 1992). For example annual litter fall, monitored with floating traps, was 369 -580 $g.m^{-2}$ in a NSW river red gum swamp (Briggs and Maher 1983), while Campbell and Fuchshuber(1994) measured 310 $g.m^{-2}$ litter accession to a Victorian temperate forest stream. However, litter fall does not necessarily equate to benthic resource availability. Leaf litter accession to the stream can be delayed after leaf fall, until wind action or water currents transport it into the stream bed (Webster and Meyer 1997).

The high flow variability at the Macquarie sites is likely to impact on benthic litter accumulation. The sudden increase in discharge after heavy rain would initially suspend dry leaf litter accumulated in the channel, and then transport it downstream. Although small leaves were expected to be more buoyant than larger leaves (Watson and Barmuta 2010), in moderately flowing water the smallest and largest leaves had similar flotation times. While all leaves were significantly more buoyant in still water, laboratory conditions do not accurately replicate field conditions, where completely still water is unlikely. However, it was noted that leaf leachates formed a surface film on the still water in the buoyancy trial, probably retarding water absorption by the leaves. This may influence litter availability for biota in remnant pools in the Macquarie River.

Based on the leaf buoyancy trials, it was expected that there would be more eucalypt leaves in Tooms River, trapped by the abundant woody debris. Smaller *Leptospermum* leaves were expected to remain suspended in the water column by the constant flow, and hence be transported downstream rather than stored in the benthos. As expected, eucalypt leaves were more abundant in Tooms River than at the Macquarie sites (Table 4.12), reflecting the close proximity of eucalypts to the Tooms River channel. Eucalypt leaves were least abundant in the benthos at IF, where litter retention may be lower due to the uniform substrate size and the lack of boulders and coarse woody debris. In contrast, the Tooms River sites appeared to be highly retentive. A pilot study showed that 44 of 80 marked eucalypt leaves (A. Watson, unpublished data) were retained within 50 m of release at TL. Marked leaf fragments from this trial were collected 11 months later in benthic litter samples from the same reach.

Leptospermum leaves were less abundant in the channel than on the banks at all sites. Litter input to the stream would be expected to decrease with the reduction in wetted channel during drought (Bond *et al.* 2008). Although *Leptospermum* plants overhang the channel at all sites, the low flow at the Macquarie sites would have prevented movement of these leaves and *Acacia* phyllodes into the channel, where the river stage height controls the accession of *Acacia* and *Leptospermum* leaves into the stream channel. The leaves fall directly below the shrub layer and are only carried into the water column at CB when this area is inundated with water (Fig. 4.12). At the downstream site, IF, and at the Tooms sites, *Acacia* and *Leptospermum* overhang the stream channel, potentially increasing accession to the benthos.

Fig.4.12 Orange *Acacia* phyllodes and yellow *Leptospermum* leaves fall onto the rocky substrate beneath the riparian vegetation at CB. Buoyant *Leptospermum* leaves float with the rising water, while *Acacia* phyllodes remain in the benthos.

The longer flotation time of *Leptospermum* leaves at slow flow rates would lead to downstream transport rather than retention within the reach, except when the flow is so low that the leaves remain in the reach for an extended time. This could explain the higher *Leptospermum* leaf abundance at IF, where the low gradient reduces the flow velocity. The abundant macrophytes at IF could also trap leaf litter (Quinn *et al.* 2007). Less buoyant *Acacia mucronata* phyllodes and larger eucalypt leaves are more likely to be trapped behind rocks and debris (Steart *et al.* 2002), increasing their abundance in the benthos. At the Macquarie sites, eucalypt leaves are more likely to be carried into the channel by wind, because these trees are distant from the channel and direct accession is reduced by the dense shrub layer.

Woody litter was more abundant in the benthos at the Macquarie sites than at the Tooms sites (Table 4.14), which was surprising given the obvious coarse woody debris in Tooms River. However, the benthic woody litter at the Macquarie sites tended to be small fragments, which may be transported in the water column, whereas discharge at the

Tooms sites is rarely high enough to move large woody debris in the channel.

Similar factors influenced woody fruit abundance. The overhanging vegetation was expected to deposit most *Leptospermum* capsules into the stream channel at the Tooms sites, but BB generally had the lowest benthic mass of *Leptospermum* capsules, except when higher discharge extended the wetted channel close to the riparian vegetation. However, the high abundance of riparian *Leptospermum* capsules at IF and CB in summer 2006-07 did not translate to high benthic capsule mass. Instead, this was highest after the 2007 spring spate, declining with the peak discharge in September 2007. This suggests that moderate flow carries litter, particularly heavier fruit capsules, into the stream channel, whereas high flow flushes fruit downstream.

While the root zone trapped *Leptospermum* leaves and fruit capsules at the Tooms River sites, this was not reflected in benthic litter composition. In contrast, *Acacia* phyllodes were abundant in benthic litter, but not in the root zone, while *Acacia* fruit had similar mass in both benthic and root zones. This was unexpected, as *Acacia* phyllodes and pods are a similar size and shape, and would be expected to perform similarly. Maximum fruit mass for all species in the root and benthic zones was correlated with periods of moderate flow in Tooms River, when the root zone was inundated.

4.6 Conclusion

The predicted influences of individual site characteristics on allochthonous and autochthonous resource abundance were listed in Table 4.1. The flow regime was predicted to influence the accumulation of benthic detritus in both rivers, with the highest benthic OM in Tooms River, due to the greater abundance of woody debris and overhanging riparian vegetation. High nutrient concentrations and low light levels were expected to increase the abundance of heterotrophic biofilms in

Tooms River, and lead to increased decomposition rates, while the variable flow regime was expected to be the main driver of biofilm abundance in the Macquarie River. However, there were some surprising results.

Although biofilm abundance was highest at the Tooms River sites, the chlorophyll *a* concentration was greatest at the upstream Tooms site, TL. At this site, autotrophic biofilms and cyanobacteria dominated the biofilms, although the high turbidity and over-hanging riparian vegetation were expected to suppress algal growth. The high algal biomass expected at the downstream Macquarie site, IF, did not eventuate. Heterotrophic biofilms were most abundant here, despite the high light levels observed at this site. Both cellulose decomposition and leaf litter decomposition were highest at the upstream Tooms site, TL, although autotrophic algae dominated the biofilms, rather than the bacteria and fungi expected at this site. Against expectations, the seasonally reversed flow regime of the Tooms River sites was not reflected in reversed seasonal abundance of biofilms and chlorophyll *a*. There was no seasonal variation in Tooms River in either biofilm AFDM or chlorophyll *a*, in contrast to the significant seasonal variation at the Macquarie sites.

As predicted in Table 4.1, more benthic litter was retained in Tooms River than in the Macquarie River, with similar abundances at the two Tooms sites. Although transported litter was restricted at TL by proximity to the dam, this was compensated by the presence of abundant woody debris and trailing vegetation, which reduced the water velocity and retained organic material, even at moderate discharge (Fig.4.13). Large rocks also retained detritus at both sites in this river.

Fig. 4.13 Trailing vegetation and fallen woody debris at TL retain detritus and reduce the water velocity. The white bands on the rock are dry protozoan colonies at two different discharge levels.

Regulation effects on water quality were less pronounced at the downstream Tooms site, BB, with input from minor tributaries diluting the turbid flow from Tooms Lake. In addition, the canopy was more open with less woody debris, although mature eucalypt trees extended to the waterline, in contrast to the shrubby riparian vegetation of the Macquarie sites. However, plant detritus contributed by the riparian vegetation was augmented at BB, by litter transported from further upstream.

This contrasts with the downstream Macquarie site, IF. Although both downstream sites have a similar grazing history, the river channel at IF is confined and incised, with established macrophyte beds. The shallow stream banks were inundated at moderate discharge, increasing litter movement from the banks to the benthos, while more litter was retained within the reach at low flow. However, the upstream broadwater pool may restrict replacement of flood-scoured litter, potentially reducing sediment and nutrient flow to the downstream Macquarie River.

Future research should focus on the factors influencing the poor water quality in Tooms River. This is a domestic water supply source and the persistent high turbidity and frequent algal blooms are a concern for human health. Nutrients (total N and P) were consistently higher in Tooms River than in the unregulated Macquarie River (Table 4.8). The source of these nutrients should be established in a long-term study, covering both high and low lake levels. This could determine whether the high nutrient concentrations are due to disturbance of the lake sediments when the lake is low, preventable sewage discharge from the shack community, or another source.

Equally important is higher taxonomic resolution of the Tooms River biofilm communities than was possible within the time constraints of this project. Cyanobacteria and diatoms appeared to dominate biofilms in this river, but fungal and bacterial abundances were not measured except by the comparative ratio approach of the autotrophic index (Section 4.4.1.3). Biofilm samples covering the two years of this study were preserved for algal cell counts, which could provide valuable information, given adequate resources. However, longer term monitoring is required to determine if the biofilm communities suggested by this study were a function of the drought and low water levels in the lake, or a persistent feature of this river.

Chapter 5 Macroinvertebrate community responses to flow regulation and drought.

5.1 Abstract

Regulation of the flow regime has been shown to influence the abundance and species composition of the invertebrate community. Macroinvertebrate communities at two sites on each of the regulated Tooms River and unregulated Macquarie River, in eastern Tasmania, were sampled over two years, coinciding with a supra-seasonal drought The invertebrate fauna at the study site nearest to the Tooms Lake dam was depauperate and dominated by snails, mites and chironomids, as reported by many studies. The downstream regulated site had a more diverse fauna than expected, and was more similar to the unregulated Macquarie River sites than to the upstream Tooms site. However, some taxonomic differences from the Macquarie River sites remained, and the seasonal variation in taxonomic composition which typified the Macquarie sites was absent. While the invertebrate communities in the two rivers were expected to converge to a common assemblage of slow-flow specialists as the drought intensified, the invertebrate taxa in the regulated river became less similar to the unregulated river fauna, demonstrating a lack of resistance to disturbance.

5.2 Introduction

Aquatic invertebrates play a major role in nutrient cycling in stream ecosystems. They consume organic material, algae, fungi and bacteria, and are thought to be pivotal to the processing of terrestrial leaf litter in forested streams (Hynes 1970a; Fisher and Likens 1973; Cummins and Klug 1979; Vannote *et al.* 1980; Cummins *et al.* 1984; Malmqvist 2002). They are also an important component of the food web for higher invertebrate and vertebrate predators (Boulton and Lake 2008).

Although the flow regime may be the most important influence on ecological processes (Lancaster 2008), invertebrate community structure and abundance may depend on the interaction of the flow regime with factors such as land use practises, which influence water quality, and habitat and resource availability. Connell (1978) proposed that the disturbance regime was the main driver of species diversity in tropical rainforest and coral reef communities. This concept has been expanded to explain species diversity in stream ecosystems (Ward and Stanford 1983a; Stanford and Ward 1993), although Reice *et al.*(1990) and others have questioned the presence of the necessary competitive hierarchies in stream communities. However, this is based on a high diversity of habitats within a stream, where the varying hydraulic stress associated with different substrate sizes reduces the potential for colonisation and consequent competition (Statzner and Higler 1986), and the probability that predictable disturbances, such as snow melt or regular summer intermittency will maintain a non-equilibrium state (Reice *et al.* 1990).

Nevertheless, the role of natural disturbance in the structure of aquatic invertebrate communities has been well documented (see reviews on the role of floods (Death 2008) and droughts (Boulton and Lake 2008)). The natural flow regime can apply strong selection pressure on invertebrate species resistance to disturbance (Poff *et al.* 1997; Lytle and Poff 2004; Lytle 2008). However, McMahon and Finlayson (2003) proposed that augmentation of summer low flows in many regulated rivers, which they term “anti-droughts”, would have more effect on biota in naturally variable Australian streams than the droughts which are part of normal cycles.

5.2.1 The effects of flow regulation on aquatic invertebrates

Petts’ (1984) 3rd-order effects of flow regulation focus on the effects on aquatic biota, which are summarised in Figure 5.1. Since his review, a

number of studies have been broadly consistent with these predictions. For example, Englund and Malmqvist (1996) recorded reduced macroinvertebrate species diversity below Swedish dams.

In temperate Australia, Nichols *et al.* (2006) recorded different invertebrate assemblages upstream and downstream of multiple impoundments in the Australian Capital Territory (ACT). Sensitive taxa (Ephemeroptera, Plecoptera, Trichoptera and Coleoptera), as defined by Chessman (1995) were less abundant than predicted by the AUSRIVAS rapid assessment method (Coysh *et al.* 2000) at the regulated sites, in which mites, oligochaetes and chironomids were more abundant. Similarly, Growns and Growns (2001) found different taxa in regulated and unregulated Hawkesbury-Nepean River sites. In their study, caddisflies, dragonflies and mayflies typified unregulated sites, while stoneflies were absent from the regulated sites, although the natural longitudinal changes in invertebrates between upstream and downstream sites may have influenced their results. By contrast, Reich *et al.* (2009) found more taxa at regulated sites on the south-eastern Australian Broken-Boosey Creek system, and also more rheophilic taxa such as Baetidae, Hydropsychidae and Simuliidae. They attributed this to the perennial flow regime in their regulated sites. Their unregulated sites contained taxa typical of ephemeral systems.

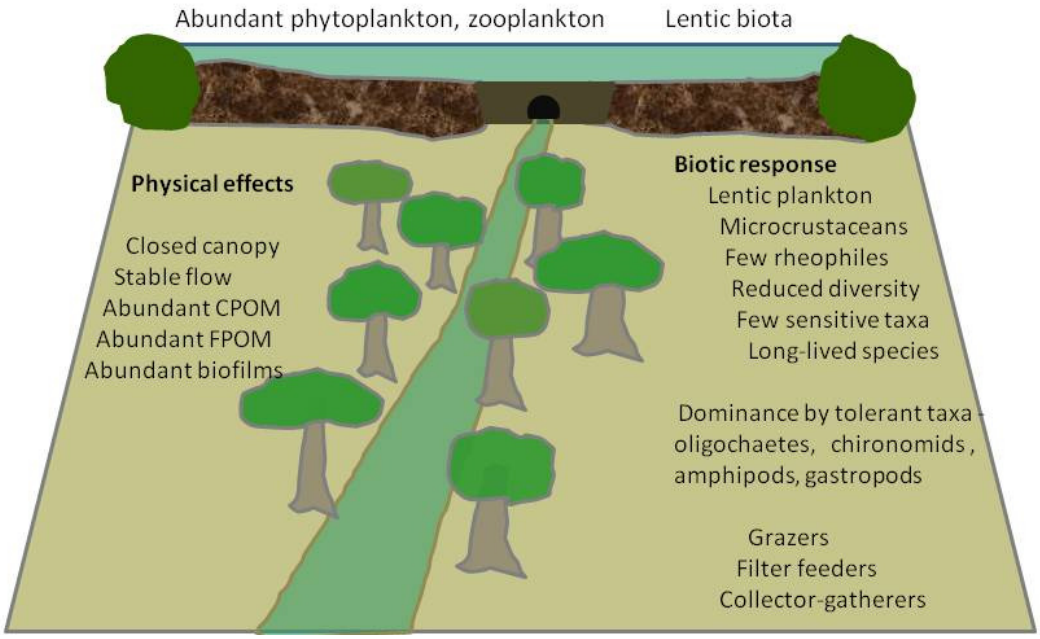


Fig.5.1 Predicted response of the invertebrate community structure to the observed physical parameters of Tooms River, based on references cited in Petts (1984). CPOM and FPOM refer to coarse and fine particulate organic material, respectively.

In addition, several studies have explored mayfly abundances in regulated streams, because mayflies are one of the taxa considered vulnerable to disturbance (e.g. Pardo *et al.* 1989; Ward and Garcia de Jalón 1991; Petts *et al.* 1993). Caenidae and some *Baetis* spp. (Baetidae) typified lentic habitats in regulated North America streams, rather than the rheophilous species expected in unregulated streams (Brittain and Saltveit 1989). Ward and Garcia de Jalón (1991) also found that some *Baetis* spp. increased in abundance below deep release dams in Spain and Colorado, but this was restricted to species tolerant of low temperatures.

Petts (1984) emphasised the confounding effects of the altered thermal regime downstream of many dams, with the strongest effects on species distribution linked to hypolimnial releases from deep reservoirs. For example, Ward and Stanford (1979) suggested that the dominance of taxa without aerial life stages below dams in many studies is due to the lack of thermal cues for metamorphosis and emergence.

5.2.2 The effects of drought on aquatic invertebrates

There have been few well-designed studies of the impact of drought on aquatic invertebrate communities, largely because of the unpredictable nature of droughts, while time lags may hide impacts on species diversity (Lake 2000). Lake (2003) distinguished between the effects of regular seasonal droughts and irregular supra-seasonal droughts. Seasonal droughts are typical of Mediterranean climates, where cessation of flow is relatively predictable and invertebrates are adapted to intermittent flow (Gasith and Resh 1999). Supra-seasonal droughts, by contrast, are less predictable ramp disturbances, with increasing intensity over time and slow recovery. Supra-seasonal droughts have greater impact on invertebrate communities than seasonal droughts (Boulton 2003; Lake 2003), potentially compromising terrestrial stages of amphibiotic invertebrates and future cohorts (Boulton and Lake 2008).

Aquatic biota can show a stepped response to drought, with major changes to species abundance as thresholds are crossed (Boulton 2003), which are linked to habitat availability as the water level falls (Fig. 5.2). As the stream channel contracts, the first impacts will be on species which rely on fringing macrophytes for food or habitat. These are frequently the least common taxa. Predation from fish or birds on surface-dwelling species may increase with the loss of macrophytes for protection (Boulton 2003). The loss of fast flowing channel sections will impact on species which rely on flowing water for recolonisation from invertebrate drift, or need well oxygenated water (Boulton 2003), while invertebrates can be stranded in isolated riffle patches as the water level falls (Extence 1981; Stanley *et al.* 1994). Many of these species are poor dispersers (Boulton and Lake 2008). Figure 5.2 summarises the impacts of progressive drought stages on the macroinvertebrate communities, as reported by the references listed in Table 5.1.

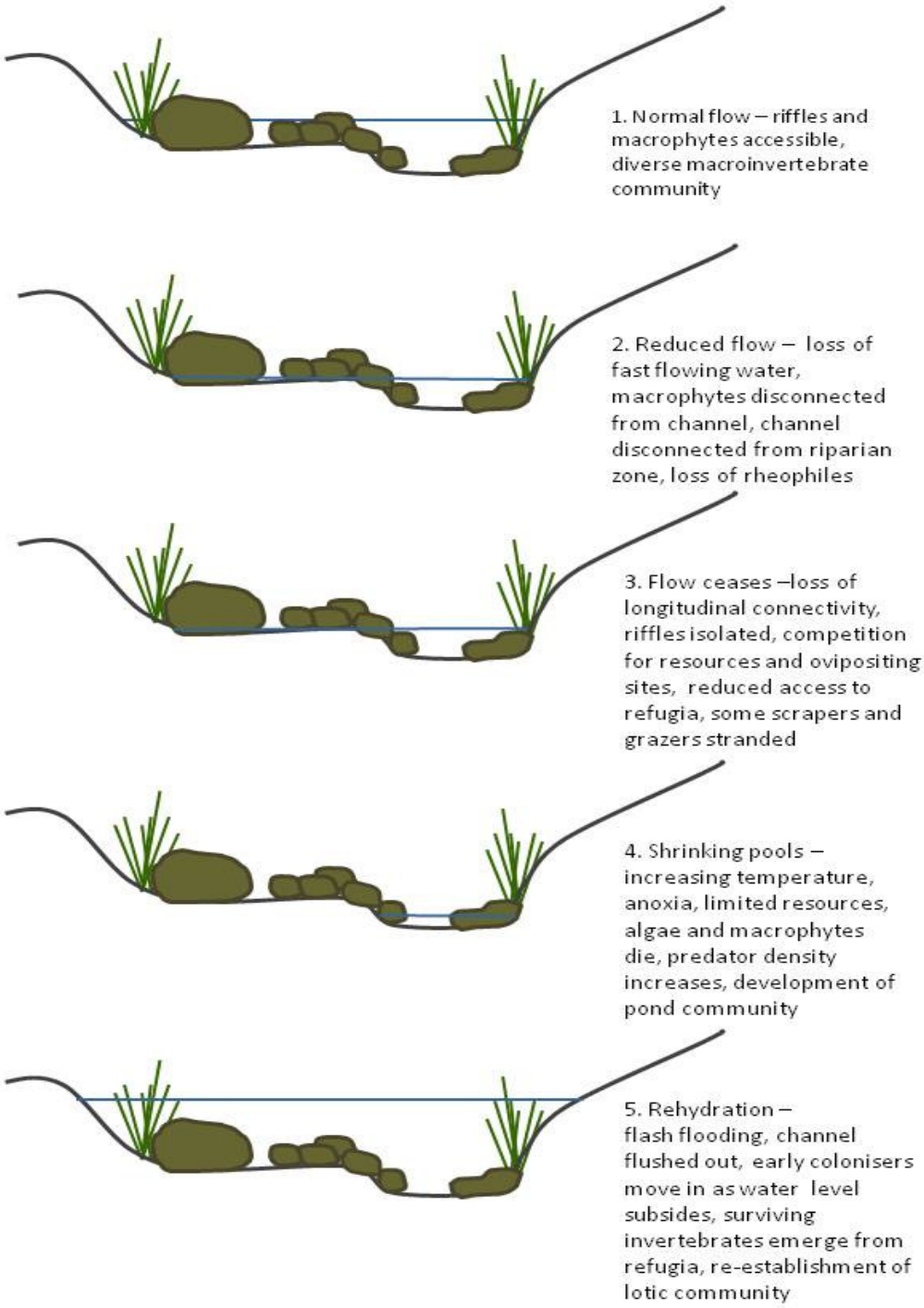


Fig. 5.2 Resources, refugia and flow conditions alter as the water level changes with drought, with impacts on macroinvertebrate habitat availability and food resources (modified from Matthews (1998)). Rehydration can be accompanied by flash flooding where hydrophobic soils increase runoff (e.g. Cerda *et al.* 1998). References citing the effects noted in each panel are listed in Table 5.1.

Table 5.1 The ecosystem processes in Fig. 5.2, and the peer-reviewed literature referred to by the numbered labels

Ecosystem process	Citing references
2 - Reduced flow	Boulton (2003); Boulton and Lake (1992b; 2008); Castella *et al.* (1995); Dewson *et al.* (2007): Matthews (1998)
3 – Flow ceases	Angradi (1999); Bond *et al.* (2008); Boulton (1989); Extence (1981); Lake (2000); McIntosh *et al.* (2002); Stanley *et al.* (1994); Stanley *et al.* (1997); Velasco and Milan (1998); Williams and Hynes (1977); Wood and Petts (1999); Wright (1992)
4– Shrinking pools	Acuña *et al.*(2005); Bogan and Lytle (2007); Bond *et al.* (2008); Boulton (1991); Boulton and Lake (1992b, c; Boulton and Lake 2008); Boulton *et al.* (1992); Chessman and Robinson (1987); Extence (1981); Ladle and Bass (1981); Stanley *et al.* (1994); Stanley *et al.* (1997); Towns (1983, 1985, 1991)
5- Rehydration	Boulton (2003); Boulton and Lake (1992b, c); Burch *et al.* (1989); Cerda *et al.* (1998); Fritz and Dodds (2004); Harrison (1966); Lake (2000); Stanley *et al.* (1997)

Decreased flow reduces nutrient transfer and isolates periphyton, which impacts on resources for filter feeders and grazers (Boulton and Lake 1992b). However, highly tolerant water column feeders, such as Culicidae and some other dipteran larvae, may be advantaged by the reduced competition for resources such as bacteria and FPOM (Boulton 1989; Boulton and Lake 1992b; Acuña *et al.* 2005). The loss of flow may also impact on food resources for species which prey on drifting invertebrates (McIntosh *et al.* 2002). In addition, physical habitat changes resulting from increased deposition of sediments (Wright 1992)

can smother interstitial spaces, reducing access to food sources (Angradi 1999; Wood and Armitage 1999) and can clog gills of invertebrates (Wright 1992).

A lentic invertebrate community may develop in pools, some invading from farm dams (Lake, unpublished data, cited in Boulton and Lake 2008). Invertebrates in slowly contracting pools are less vulnerable to drought than run or riffle species, but a pool community will eventually dominate (Stanley *et al.* 1997). As pools continue to shrink, water quality declines, eliminating predatory fish (Boulton and Lake 1992b; Stanley *et al.* 1994; Acuña *et al.* 2005) and limiting the insect community to highly tolerant species (Towns 1991), dominated by Diptera, air-breathing Hemiptera and some Coleoptera (Bond *et al.* 2008; Boulton and Lake 2008). Collector-gatherers will replace shredding invertebrates in pools (Maamri *et al.* 1997; Bogan and Lytle 2007) and scrapers will become more important in litter breakdown (Boulton 1991; Maamri *et al.* 1997). Limited food resources in an extended drought can lead to an overall decrease in detritivore abundance (Bogan and Lytle 2007). However, a few Ephemeroptera and Trichoptera are able to survive these conditions (Towns 1983, 1985). Generally, the most tolerant taxa are also the most mobile and can move to larger pools to escape the worst drought effects (Williams and Hynes 1977; Boulton 1989; Velasco and Millan 1998), although riffle specialists may be lost from a reach after several years of drought (Stanley *et al.* 1997).

Increased invertebrate density in pools (the “predator soup” of Boulton and Lake (1992b)), intensifies predator-prey interactions and competition for resources (Stanley *et al.* 1994), with abundant prey attracting predators (Extence 1981), including Hemiptera, Coleoptera and Odonata (Boulton and Lake 1992b; Stanley *et al.* 1994; Acuña *et al.* 2005), and terrestrial vertebrates (Lake 2003). Vertebrate scavengers, ants and semi-terrestrial Coleoptera can also consume stranded

invertebrates in dry sections of the stream bed (Stanley *et al.* 1994; Lake 2003).

The tolerance of individual species to warmer temperatures, reduced oxygen saturation and poor water quality will partially determine species succession in remnant pools (Gasith and Resh 1999), but variation in species composition will also depend on the duration and intensity of drought, the original condition of the stream channel and the number and type of refugia present (Boulton and Lake 2008). However, the presence of refugia does not always ensure a species' survival (Churchel and Batzer 2006). As physical conditions vary between pools and over time, so can invertebrate species composition (Meyerhoff and Lind 1987; Stanley *et al.* 1997).

Lake (2003) hypothesised that invertebrates from intermittent streams should be more able to withstand drought (their *resistance*) than biota in permanent streams. The *resilience* of individual species (their ability to recover from the disturbance) (Gasith and Resh 1999; Lake 2000) will be influenced by the channel geomorphology (Stanley *et al.* 1997), the duration of the drought, drought frequency, the presence of upstream or downstream refugia and the extent of anthropogenic impact (Boulton and Lake 2008). Bond *et al.* (2008) assert that river regulation will exacerbate drought effects, while deteriorating water quality can also confound drought effects in regulated rivers (Lind *et al.* 2006). However, the patterns of drying will be influenced by the different morphology of stream sections or rivers (e.g. riffles or deeper channels), and are likely to be a major factor in biotic responses to drought and recovery (Boulton and Suter 1986). The impacts of flow reduction will also depend on whether the habitat available at low flow is the result of reduced wetted channel width or reduced stream depth (Dewson *et al.* 2007).

5.2.3 Aims of this study

The original aim of this study was to examine the macroinvertebrate communities of an unregulated river with that of a regulated river, where the effects of the "anti-drought" flow regime of McMahon and Finlayson (2003) could be assessed without the confounding effects of thermal changes from impoundment or differences in land use practises between catchments. Unfortunately, the study coincided with 2 years of a supra-seasonal drought. During this period, the unregulated Macquarie River had intermittent flow. In contrast, flow was continuous in the regulated Tooms River, but was unusually low in winter and lower than average in summer, with restricted irrigation releases (Ch. 2.6.2). The initial collection round in January 2006 provided an example of the faunal composition that prevails in these rivers at the end of a year of average rainfall and temperature (Bureau of Meteorology 2010).

Invertebrate communities in Tooms River were expected to be modified by the impoundment, with low diversity and dominance by tolerant species (Petts 1984; Poff and Zimmerman 2010). Some recovery was expected at the downstream Tooms site, with dilution of the effects of the dam by input from tributaries, as found by Storey *et al.* (1991) and Nichols *et al.* (2006), and with recolonisation from the adjoining Macquarie River. On this basis, it was considered likely that the invertebrate community at the downstream Tooms site would be similar to that of the Macquarie River, particularly to the downstream site, IF. The Macquarie River invertebrate community was predicted to have higher diversity than Tooms River, reflecting its disturbance regime (Townsend *et al.* 1997b) and to show the strong seasonality typical of intermittent rivers (e.g. Boulton and Lake 1992c).

Based on the studies reviewed above (Fig. 5.2, Table 5.1), it was predicted that the drought would have similar impact on both rivers,

with invertebrate communities converging on a common structure, dominated by tolerant taxa (e.g. Diptera) and low flow specialists such as Hemiptera, with increased predator abundance but few shredders or scraper-grazers. However, regulation of the flow regime can produce similar effects to drought in some river systems, so that the invertebrates in Tooms River may be resistant to periods of low flow.

5.3 Methods

5.3.1 Field protocol

Nine macroinvertebrate community samples were collected with a kick net (250 µm mesh, 350mm x 250mm opening) at each site at approximately quarterly intervals, from January 2006 until November 2007. Samples were collected with a 20 second kick at a single stationary point, and preserved in 70% ethanol. A kick net was the only sampling method possible given the large cobble and boulder substrate of most sites, which rendered quadrat-based sampling unfeasible. All samples were randomly collected from riffle zones where possible, since initially the study was designed to focus on flow events in the habitat most vulnerable to flow regulation (i.e. riffles). As the drought progressed, sampling continued in the fastest flowing section of the channel at each site, but, inevitably some Macquarie River samples were collected from remnant pools when flow was very low. Flow velocities were also very low in Tooms River in the later part of the drought.

In the laboratory, the samples were rinsed into a 500 µm sieve. Macroinvertebrates were hand-picked under a dissecting microscope for all 9 samples for the first 3 collection dates, then from 5 of the 9 kick samples for the remainder of the study, because initial analyses indicated that 5 samples captured the community composition as well as 9 samples. Invertebrates were stored in 70% ethanol with glycerol. Initially invertebrates were identified to the lowest taxonomic level

allowed by available keys (Appendix 3), excluding Acarina which were classified to morphospecies, and Oligochaeta, Nematoda, Copepoda, Isopoda and Ostracoda, classified to class or order. However, time constraints necessitated identification of insect taxa to family level for sample rounds 4 to 8, with mites identified to order. Again, preliminary analyses indicated that differences between sites and times remained at this coarser taxonomic resolution. Analysis of similarity (ANOSIM) of species level data for the first 3 collection rounds indicated there were significant differences in species abundance between rivers (Global R: 0.302, $p < 0.001$) and between each pair of sites (all $p < 0.001$). Family level taxonomic resolution is common in biomonitoring programmes such as AUSRIVAS (Australian River Assessment System; Coysh *et al.* (2000)), which is based on the British River Invertebrate Prediction and Classification System (RIVPACS; Clarke *et al.* (2003)). Moreover, family level resolution has been used in several recent studies (e.g. Bogan and Lytle 2007) . The high abundance of small Chironomidae (Diptera) made routine identification to sub-family impractical, so they were classified by functional feeding group as predatory Tanypodinae or collector-gathering non-Tanypodinae. Functional feeding groups (collector-gatherers (hereafter collectors); filter feeders (filterers); predators; scrapers; and shredders) were determined according to published Australian references (Chessman 1986; Growns and Davis 1994; Gooderham and Tsyrlin 2002) augmented with direct observations of mouthparts and feeding structures where necessary. Ephemeroptera, Plecoptera and Trichoptera (EPT taxa) were also enumerated, because the percentage of EPT taxa is often considered an indicator of the 'health' of a river system (e.g. Wallace *et al.* 1996).

5.3.2 Data analysis

Macroinvertebrates were enumerated from all 9 samples for the first 3 sample rounds, but from 5 of the 9 samples for subsequent sample rounds, as detailed above. Therefore, data analysis was restricted to 5

randomly selected samples from the original 9 samples for the first 3 sample rounds, to prevent biasing by sample number, with analysis of all rounds at family level or lower taxonomic resolution, as above.

5.3.2.1 Univariate analyses

The total number of animals in each taxon was summed within each sample date for each site, prior to the computation of diversity indices. This allowed for stronger descriptors of the site-level diversity than averaging across measures computed at the level of replicates, and provided a fully balanced design for analysis. The negative logarithm of Simpson's index was used to calculate diversity. Simpson's index, *D*, is given by:

$$D = \sum_{i=1}^{S} p_i$$

where S is the number of taxa, and p_i is the proportion of taxon i in a given sample unit. Simpson's index is generally regarded as one of the most meaningful and robust indices of diversity, although it is more usually expressed as $1 - D$ or $1/D$ so that it increases with increasing diversity (Magurran 2004); $-\log_e(D)$, however, has fewer variance problems than $1/D$, and is independent of the number of individuals in the taxon (Magurran 2004). The index increases as the number of taxa increase and as their relative proportions become more even. Evenness is often computed separately, and Simpson's evenness index, $E_{1/D}$, is given by:

$$E_{\frac{1}{D}} = \frac{1/D}{S}$$

This measure is not sensitive to species richness and varies from 0 (perfectly uneven) to 1 (perfectly even, i.e., all taxa present in the same proportions). Species richness, *S*, and total abundance, *N*, were also included in these analyses. A repeated-measures ANOVA was

conducted with flow status (regulated v. unregulated) as the between-subjects factor, and sample date as the within-subjects factor. Inspection of residuals and standard diagnostics showed no violation of assumptions for -$\log_e$ (D), $E_{1/D}$, S or log-transformed N.

5.3.2.2 Multivariate analyses

Similarity (or dissimilarity) measures are preferred for all multivariate procedures for species-in-samples data sets. The Bray-Curtis measure was selected because of its demonstrated ability to represent ecological distances in low-dimensional space (Faith *et al.* 1987; Legendre and Legendre 1998). The invertebrate family-level counts were square-root transformed prior to computing this measure to down-weight the impact of occasionally large abundances of one or two taxa. This is common practice for benthic data (Clarke and Warwick 2001), but does not unduly emphasise the contributions by occasional rare taxa as would happen with log transformation or conversion to presence-absence (Legendre and Legendre 1998).

To determine whether there were any differences in community composition between regulated and unregulated sites, randomisation tests were conducted using the *adonis* procedure in vegan (Oksanen *et al.* 2010), which is analogous to the ANOSIM (analysis of similarity) procedure of Clarke and Gorley (1993). Sample dates were treated as 'blocks', and the 1999 randomisations were restricted within these blocks to prevent inflation of the Type 1 error (Good 2000). Two additional *a priori* tests contrasted sites within each river. These were orthogonal to each other and to the main contrast of regulated versus unregulated sites.

The taxa that tended to be associated with each of the river types, and with each site were characterised using the Indicator Species Analysis (ISA) of Dufrêne and Legendre (1997). This index combines a measure of taxon abundance with one of fidelity to a group (i.e. a taxon's

tendency to be found within one group but not in another: a taxon that is unique to a group has high fidelity to that group). The correct formulation of this index is given in the appendix of Aho (2008), and it was computed using the *indval* function in the R package labdsv (Roberts 2010). This procedure also allows testing of the significance of each taxon's association with a group using randomisation, and taxa that were significant at $p < 0.05$ were tabulated.

To determine whether the sites converged or diverged in species composition over time, all replicates within each combination of site and sample date were averaged prior to computing the Bray-Curtis measure followed by an ordination by unconstrained non-metric multi-dimensional scaling (NMDS). This can provide useful displays to complement formal hypothesis tests in that the pattern of sample points is dictated purely by their degrees of biological similarity (Anderson and Willis 2003). Thus other patterns might emerge from such displays that might be masked by the constraints imposed by procedures such as canonical correspondence analysis (CCA) and distance-based redundancy analysis (dbRDA). These ordinations were carried out using the *metaMDS* wrapper function in vegan which implements at least 20 random starts (Oksanen *et al.* 2010) of the *isoMDS* function (Venables and Ripley 2002) to prevent local optima. Ordinations were also scaled so that one unit on each axis represents 1 half-change of species composition (i.e. points separated by 1 unit on the ordination, on average, differ by 50% in their species composition), and the ordinations were displayed using ggplot2 (Wickham 2009). Rare taxa which occurred as a single specimen at a site in a round were excluded from the ordination plots for clarity.

5.4 Results

Overall, there were 96 974 individual invertebrates identified in the 156 samples, from 81 taxonomic groups (Appendix 4). The presence and abundance of individual taxa varied between rivers and study sites, with

the drought impacting on the community composition at all sites (Tables 5.2, 5.3).

Table 5.2 Mean percentage (%) of the main taxa contributing to the total invertebrate abundance at the Tooms River sites on each collection date.

Collection round	1	2	3	4	5	6	7	8
Date	Jan 06 %	April 06 %	July 06 %	Nov 06 %	Mar 07 %	June 07 %	Sept 07 %	Nov 07 %
Tooms River: Site TL								
Ephemeroptera	0.14	0.05	0.16	0.00	0.36	0.09	0.36	0.00
Plecoptera	4.94	19.93	29.08	4.20	6.47	24.35	28.83	1.54
Trichoptera	0.85	1.56	0.40	0.12	1.41	0.55	0.57	1.53
Coleoptera	0.04	0.00	0.13	0.07	0.27	0.03	0.12	0.07
Chironomidae	0.78	5.56	1.82	13.32	13.30	32.56	12.04	36.08
Diptera	0.06	4.82	1.15	0.89	1.77	9.04	0.49	14.24
Hemiptera	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Crustacea	4.37	0.82	0.50	0.40	2.72	0.67	3.35	0.35
Mollusca	69.68	22.52	38.65	39.77	36.02	7.07	19.04	6.60
Acarina	10.97	5.11	10.08	12.46	17.02	15.24	12.15	6.30
Oligochaeta	3.71	0.36	0.62	0.05	4.43	0.77	0.68	1.33
Nematoda	1.98	1.36	2.53	4.31	4.44	7.07	8.93	5.18
Microcrustacea	2.31	37.55	1.24	24.30	3.48	2.27	13.27	26.47
Tooms River: Site BB								
Ephemeroptera	14.07	23.59	25.93	7.50	17.37	28.41	21.91	11.72
Plecoptera	25.74	12.94	6.57	16.91	6.19	10.36	9.34	7.50
Trichoptera	8.56	9.03	11.57	5.82	5.37	5.30	2.54	5.03
Coleoptera	6.22	6.73	3.71	10.25	5.26	3.55	7.78	2.52
Chironomidae	12.15	15.03	32.76	32.60	42.64	29.27	41.56	48.19
Diptera	3.23	3.62	4.41	8.06	6.61	10.28	2.97	11.09
Hemiptera	0.13	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Crustacea	0.00	0.00	0.17	0.25	0.09	0.05	0.00	0.36
Mollusca	18.51	22.52	3.73	6.89	5.06	4.40	4.20	4.86
Acarina	6.79	2.77	2.76	6.52	3.91	2.72	6.77	4.99
Oligochaeta	0.58	2.01	5.04	0.70	5.92	4.01	0.91	3.32
Nematoda	0.22	0.23	0.74	0.61	0.49	0.11	0.00	0.39
Microcrustacea	3.09	1.13	2.19	2.68	0.31	0.65	0.72	1.31

Table 5.3 Mean percentage (%) of the main taxa contributing to the total invertebrate abundance of the Macquarie River sites on each collection date.

Collection round	1	2	3	4	5	6	7	8
Date	Jan 06 %	April 06 %	July 06 %	Nov 06 %	Mar 07 %	June 07 %	Sept 07 %	Nov 07 %
Macquarie River : Site CB								
Ephemeroptera	34.43	3.78	2.58	16.23	8.27	0.62	1.77	20.84
Plecoptera	7.01	8.98	28.87	8.02	33.25	53.31	40.54	27.39
Trichoptera	3.22	1.39	0.96	6.19	10.17	0.17	0.63	1.91
Coleoptera	1.28	2.86	1.91	7.36	1.72	0.46	0.54	2.51
Chironomidae	21.46	1.42	10.47	11.84	19.82	16.70	31.18	26.35
Diptera	0.36	0.71	0.68	1.88	0.59	4.67	1.45	0.35
Hemiptera	3.19	0.05	0.00	0.00	0.05	0.00	0.00	0.05
Crustacea	3.64	10.76	5.76	11.87	4.64	3.16	2.19	7.16
Mollusca	19.15	65.41	43.69	25.81	13.04	14.24	18.04	0.91
Acarina	1.84	0.87	1.30	4.89	1.48	5.10	1.17	0.88
Oligochaeta	1.21	2.04	1.89	0.45	2.31	0.97	0.33	1.60
Nematoda	0.01	0.29	0.11	0.29	0.14	0.00	0.28	0.00
Microcrustacea	2.81	0.15	1.72	5.06	4.24	0.40	1.00	9.95
Macquarie River : Site IF								
Ephemeroptera	12.01	3.59	1.02	6.12	2.96	4.10	9.59	32.18
Plecoptera	1.76	4.07	7.06	1.99	3.69	3.09	1.67	4.08
Trichoptera	17.20	2.06	0.57	1.41	4.16	1.42	3.47	2.63
Coleoptera	2.93	8.13	3.69	2.40	1.12	0.34	0.86	0.60
Chironomidae	29.01	10.43	7.98	47.10	38.79	19.60	62.53	14.59
Diptera	12.09	4.75	3.70	1.71	2.45	65.58	5.72	0.79
Hemiptera	0.19	0.38	0.06	0.06	0.05	0.00	0.00	0.00
Crustacea	0.52	2.26	2.24	3.12	1.06	0.33	0.15	1.19
Mollusca	15.17	11.11	48.61	16.65	7.46	1.17	2.48	7.52
Acarina	3.01	2.03	2.50	3.48	1.18	0.43	1.40	2.71
Oligochaeta	2.14	19.07	5.73	0.71	2.67	1.60	1.34	1.37
Nematoda	0.48	2.80	0.16	1.05	1.60	0.11	2.01	1.70
Microcrustacea	2.56	24.41	14.94	14.00	32.32	2.02	7.29	30.31

5.4.1 Univariate measures

Univariate measures did not detect any significant difference between regulated and unregulated rivers, no significant effects of sample date, nor interactions with it for species abundance, *N*, species richness *S*, or evenness, *E*. There was some evidence for diversity, as measured by Simpsons Index ($-\log_e(D)$) to be higher on average in the unregulated sites, although both sites were only significantly more diverse in one sample round (April 2006) (Table. 5.4, Fig 5.3).

Table 5.4 ANOVA results for total invertebrate abundance (*N*), species richness (*S*), evenness (*E*) and Simpsons inverse diversity (-log(D)) by status (regulated or unregulated) and sample round; df = degrees of freedom, MS = mean sum of squares. The single significant effect is indicated with *.

Source	df	MS	*F*	*p*
Total abundance N				
Status	1,2	0.0929	1.080	0.408
Round	1,26	0.0663	1.158	0.292
Species richness S				
Status	1,2	15.1250	0.313	0.632
Round	1,26	9.0540	0.232	0.634
Evenness E				
Status	1,2	0.0146	6.027	0.134
Round	1,26	0.0006	0.184	0.672
*Simpsons Diversity -log(*D*)*				
Status	1,2	0.0496	33.272	0.029 *
Round	1,26	0.0007	0.052	0.821

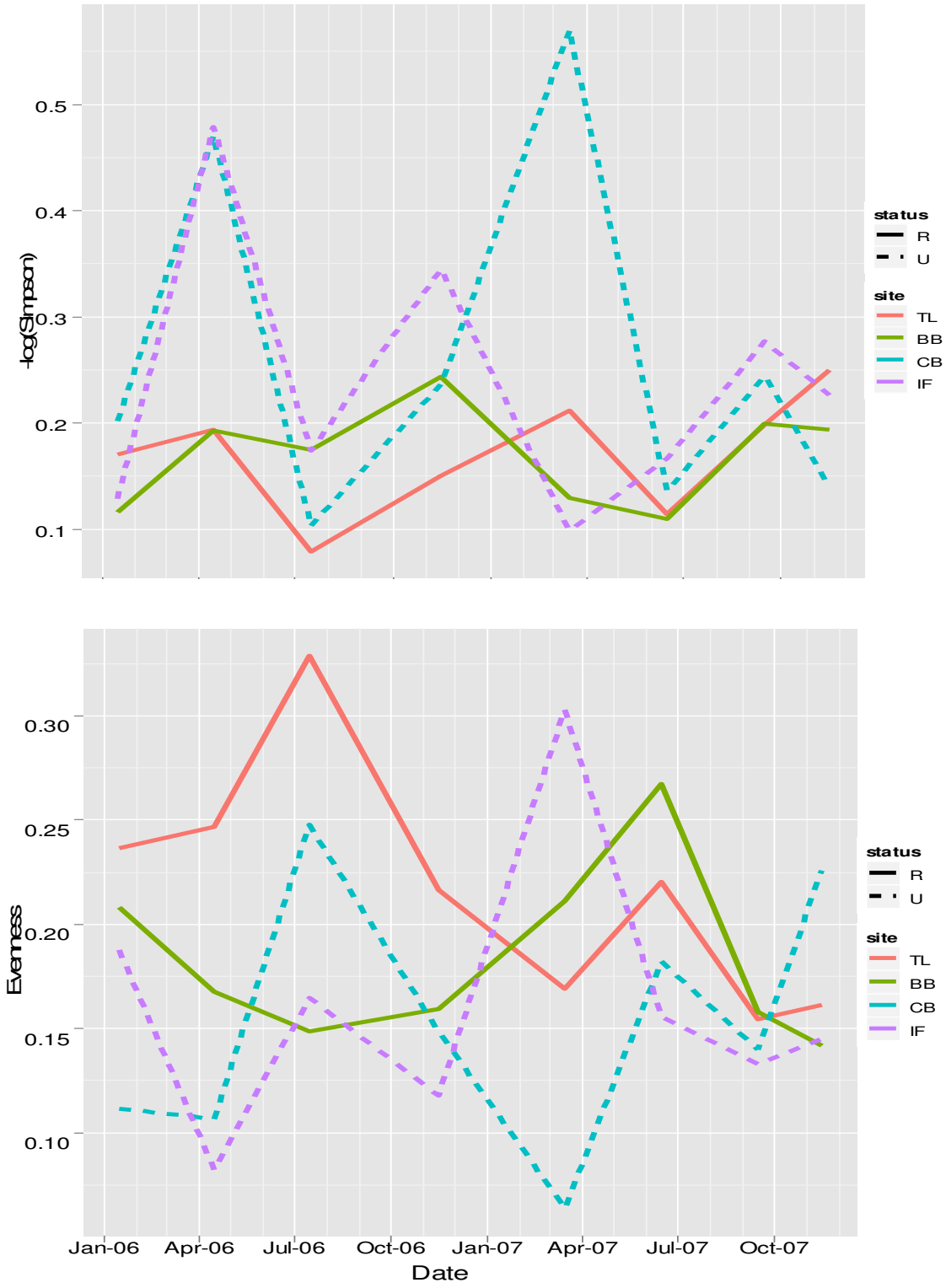


Fig. 5.3 The negative log of Simpsons diversity index ($-\log_e(D)$) (upper panel) and evenness (lower panel) of invertebrate species abundance by site and date, with regulated sites (TL and BB) shown by solid lines and unregulated sites (CB and IF) shown by dashed lines. Individual sites within rivers are indicated by the colour key.

5.4.2 Multivariate measures

In contrast to the results of the univariate analyses, the multivariate analyses detected highly significant differences in community composition (invertebrate family abundance, based on a Bray-Curtis similarity matrix) between the regulated and unregulated rivers and between sites within each river (Table 5.5).

Table 5.5 Significant differences in invertebrate family abundance between rivers and between upstream and downstream sites on each river

Source	df	MS	*F*	*p*
Regulated v unregulated	1, 154	1.3157	9.543	< 0.001
TL v BB	1, 78	2.8778	20.873	< 0.001
CB v IF	1, 76	1.0545	7.648	< 0.001
Residuals	154	0.1379	0.802	

The stress values for the 3-D NMDS plots were satisfactorily low (Table 5.6) and 4-D solutions showed no further structure than the 3-D solution. Figure 5.6 illustrates that the invertebrate communities at each site rarely overlap in the 3 dimensional space of the NMDS ordinations.

Table 5.6 Stress levels of the 3-dimensional NMDS trajectory over time

Dimensions	Stress
1	0.386
2	0.204
3	0.136
4	0.089
5	0.063
6	0.043

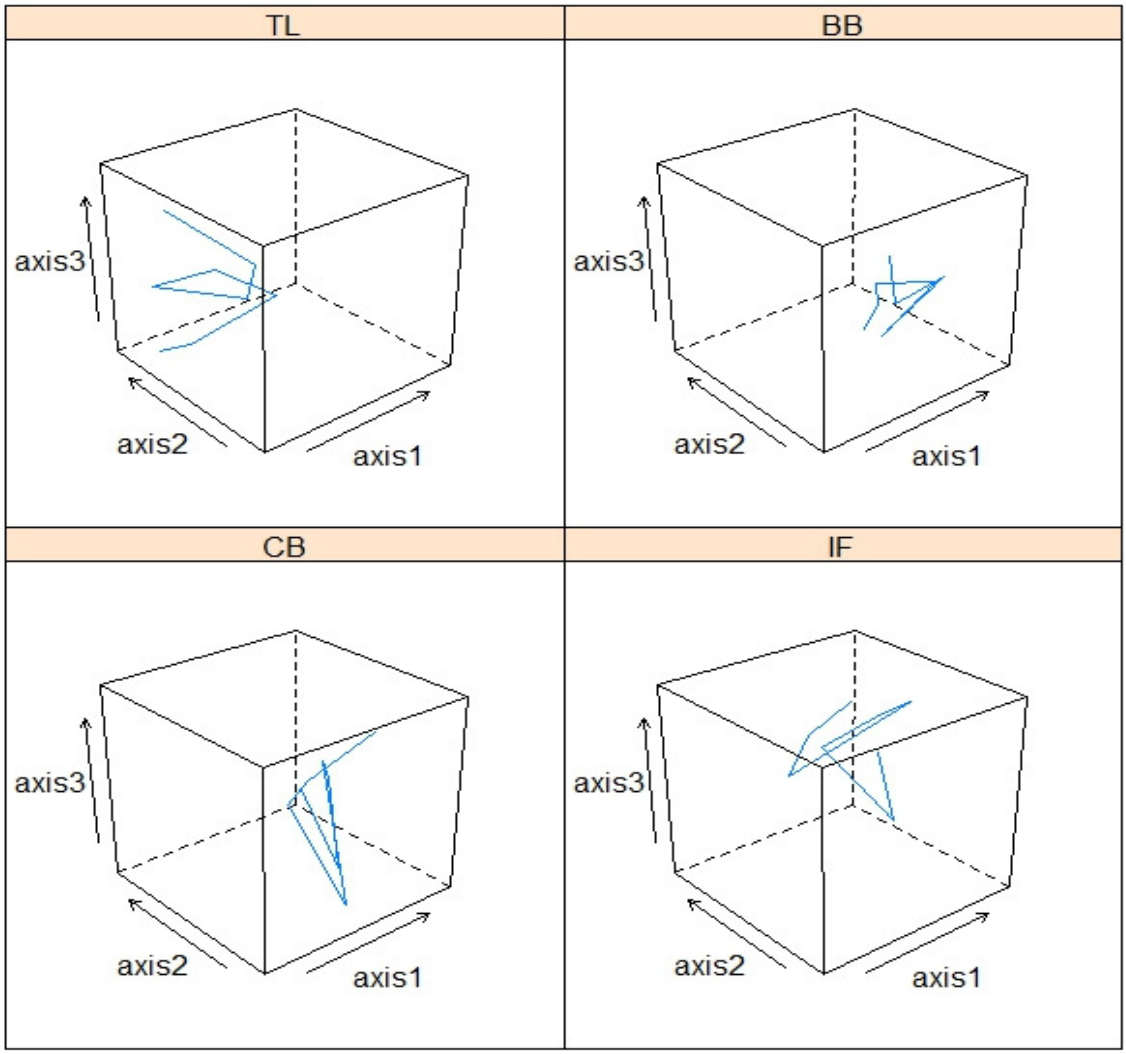


Fig. 5.4 Non-metric multidimensional scaling of the temporal abundance of invertebrate families on the 3 axes of the ordination. TL and BB are the upstream and downstream Tooms River sites; CB and IF are the upstream and downstream Macquarie sites, respectively. The blue line within each 3-dimensional data cloud shows the temporal trajectory of the invertebrate communities at each site, with each change in the vector direction demonstrating a change in the community composition between those collection dates.

For greater clarity, the vectors of the temporal trajectories of the 2 dimensional combinations of the first 3 axes of the ordination are displayed in Figures 5.5, 5.6 and 5.7, labelled with the month and year of sample collection. The upstream Tooms site, TL, occupies a completely separate position on axes 1 and 2 to the other three sites. The invertebrate communities at the downstream Tooms site, BB, partially overlap the ordinations for the two Macquarie sites (Fig. 5.5).

The community structure at TL remained distinct on axes 1 and 3, and also on axes 2 and 3, which illustrates that, rather than showing a temporal convergence towards the communities at the other three sites, the community at this site was moving towards a different structure to that present in the first, pre-drought sampling round. The community at the downstream Tooms site, BB, moved in a cycle, without significant directional change, while the two Macquarie sites both show strong seasonal trends to different community abundances (Fig. 5.6, Fig. 5.7).

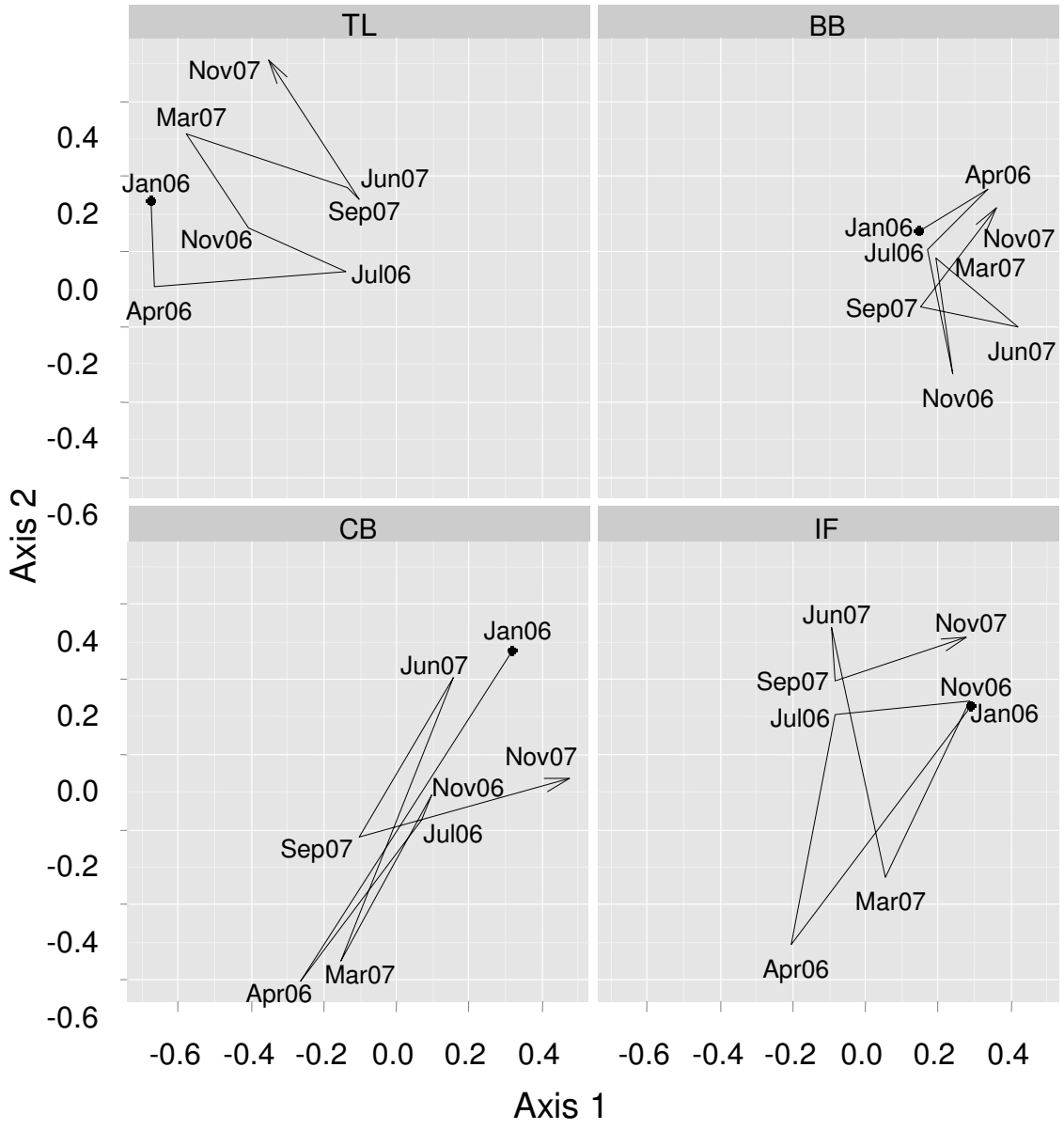


Fig. 5.5 Non-metric multidimensional scaling of the temporal trajectories of invertebrate community abundance for each study site, on Axis 1 and Axis 2 of the ordination. The vectors show the directional changes at each sample date (month, year). A black dot and arrow indicate the first and final collection round, respectively. TL and BB are the upstream and downstream Tooms site; CB and IF are the upstream and downstream Macquarie sites, respectively.

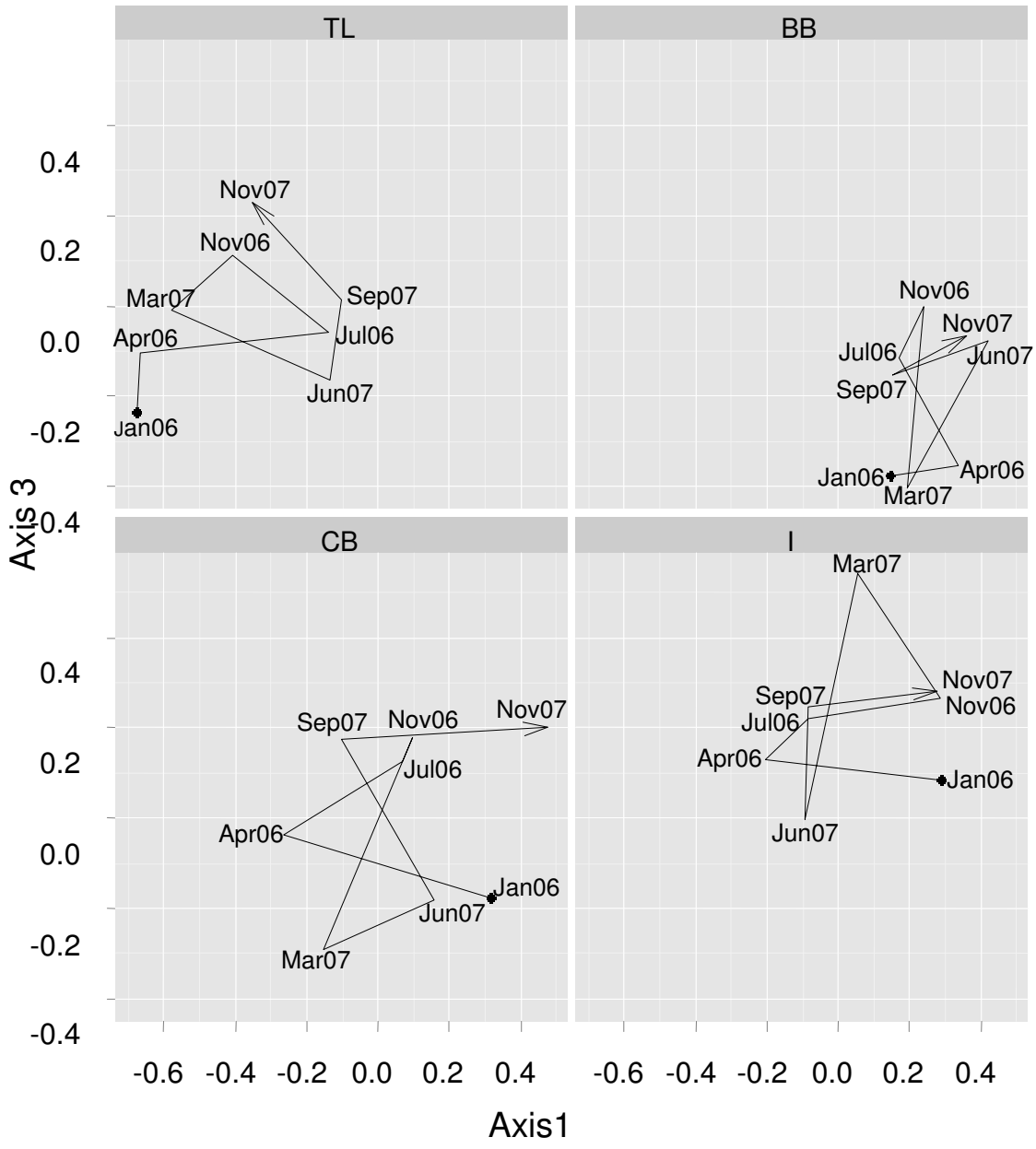


Fig. 5.6 Non-metric multidimensional scaling of the temporal trajectories of invertebrate community abundance for each study site, on Axis 1 and Axis 3 of the ordination. The vectors show the directional changes at each sample date (month, year). A black dot and arrow indicate the first and final collection round, respectively. TL and BB are the upstream and downstream Tooms site; CB and IF are the upstream and downstream Macquarie sites, respectively.

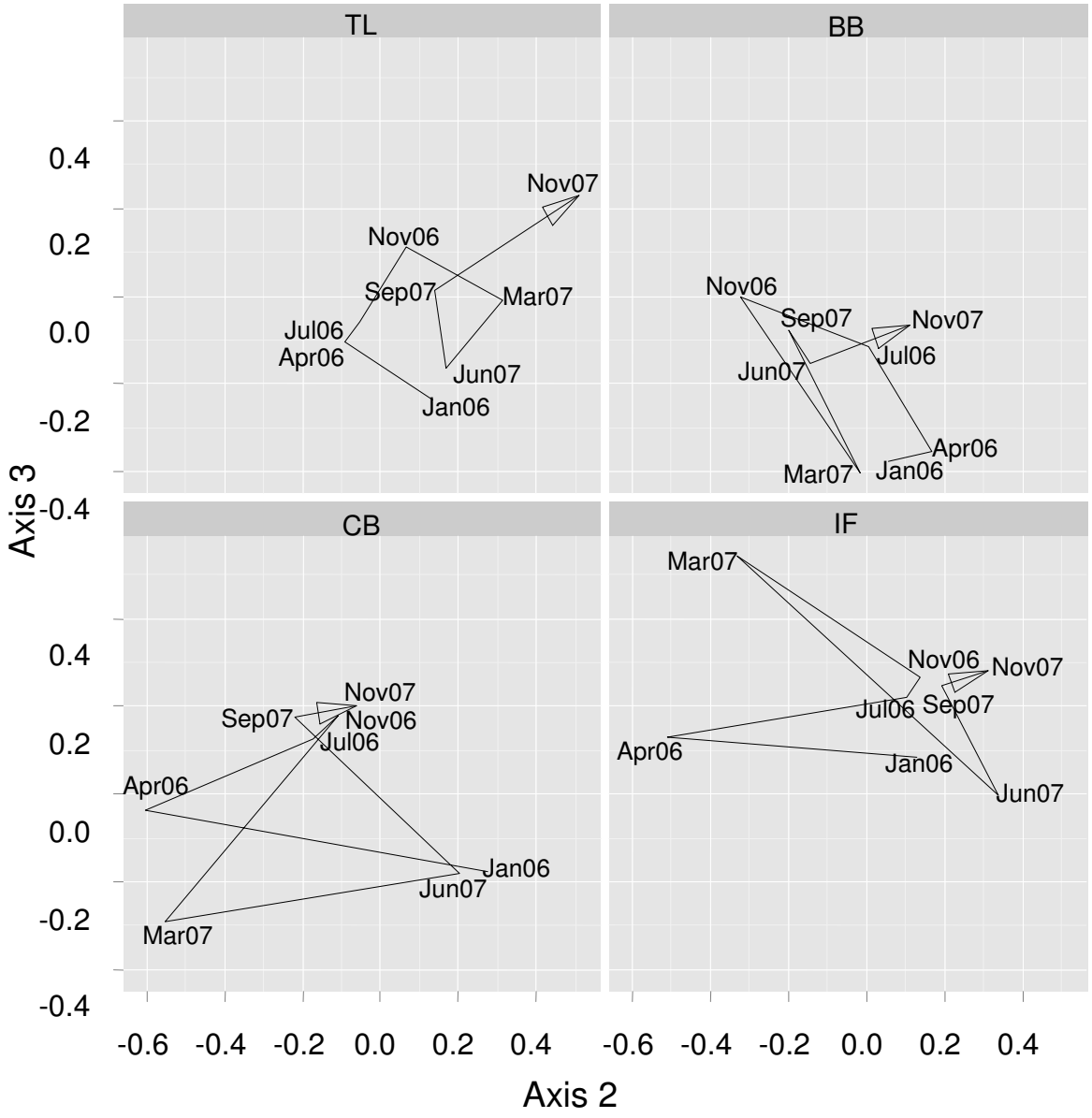


Fig. 5.7 Non-metric multidimensional scaling of the temporal trajectories of invertebrate community abundance for each study site, on Axis 2 and Axis 3 of the ordination. The vectors show the directional changes at each sample date (month, year). A black dot and arrow indicate the first and final collection round, respectively. TL and BB are the upstream and downstream Tooms site; CB and IF are the upstream and downstream Macquarie sites, respectively.

Thirty five invertebrate taxa were significantly associated with the separation between regulated and unregulated rivers in the ordination. Eighteen and seventeen taxa respectively, were indicative of the regulated and unregulated rivers (Table 5.7). There were 28 taxa which significantly differentiated between the Tooms River sites, but only 16 which separated the Macquarie sites (Appendix i). No indicator taxa occurred at more than one site.

Table 5.7 Indicator values and probability of that macroinvertebrate taxon being indicative of the regulated (R) Tooms River and unregulated (U) Macquarie River.

Taxon	River status	Indicator value	Probability
Gripopterygidae	R	0.622	0.001
Acarina	R	0.620	0.001
Ancylidae	R	0.465	0.001
Nematoda	R	0.428	0.036
Tanyderidae	R	0.392	0.001
Psephenidae	R	0.381	0.035
Hydrobiosidae	R	0.362	0.036
Baetidae	R	0.360	0.001
Physidae	R	0.349	0.001
Athericidae	R	0.336	0.001
Eustheniidae	R	0.333	0.001
Calocidae	R	0.328	0.003
Sialidae	R	0.288	0.001
Glacidorbidae	R	0.239	0.011
Philorheithridae	R	0.181	0.004
Hydropsychidae	R	0.173	0.001
Atriplectididae	R	0.115	0.008
Ceinidae	U	0.578	0.001
Tanypodinae	U	0.573	0.001
Leptophlebiidae	U	0.500	0.011
Scirtidae	U	0.316	0.002
Caenidae	U	0.283	0.001
Uramphisopinae	U	0.230	0.002
Chydoridae	U	0.213	0.009
Atyidae	U	0.205	0.001
Hirudinea	U	0.191	0.006
Sphaeridae	U	0.182	0.009
Janiridae	U	0.170	0.001
Dytiscidae	U	0.169	0.018
Synthemistidae	U	0.103	0.004
Corixidae	U	0.091	0.030
Calamoceratidae	U	0.077	0.014
Gerridae	U	0.064	0.034
Culicidae	U	0.064	0.028
Dolichopodidae	U	0.064	0.030

5.4.3 Ephemeroptera-Plecoptera-Trichoptera (EPT) taxa abundance

There were few EPT taxa present at the upstream Tooms site, TL, in most seasons. EPT taxa were most abundant at the upstream Macquarie site, CB, and the downstream Tooms site, BB. There was generally a low percentage of EPT taxa at the downstream Macquarie site, IF.

Individual EPT taxa, however, differed in their response to regulation and drought. Ephemeroptera were rare at the upstream Tooms site, forming less than 1% of the total taxa at this site in any round. Ephemeroptera were most abundant at all sites at times of lowest discharge, in winter at BB, and in summer at the Macquarie sites. Leptophlebidae were abundant at BB in most rounds and were usually more abundant at CB than at IF, but were only collected at TL in spring and autumn. Caenidae were present at all sites, but rare at BB. In contrast, Baetidae were most abundant at BB, but decreased in abundance at all sites in the last two rounds (Table 5.8).

Gripopterygidae were the most abundant stonefly at BB in round 1, with an average abundance of 127 per sample, but declined in abundance to 8 per sample in round 8. Gripopterygidae were common at CB and TL, but were least abundant at IF. They were most abundant at times of highest flow at all sites, declining as flow reduced. The Plecoptera families Eustheniidae and Notonemouridae were not collected at TL. While Eustheniidae were rare at IF, Notonemouridae were common in spring and early summer.

Table 5.8. Mean abundance of main Ephemeroptera, Plecoptera and Trichoptera (EPT) families collected per sample (n = 5) at each study site on each collection date

Collection round		1	2	3	4	5	6	7	8
Date		Jan 06	April 06	July 06	Nov 06	Mar 07	June 07	Sept 07	Nov 07
Tooms River Site TL									
Ephemeroptera	Baetidae	0.0	0.2	0.0	0.0	0.2	0.0	0.2	0.0
	Caenidae	0.2	0.4	0.4	0.0	0.4	0.8	1.2	0.0
	Leptophlebiidae	0.8	0.2	0.0	0.0	0.6	0.0	0.4	0.0
Plecoptera	Eusthenidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Gripopterygidae	34.8	288.2	126.2	36.6	25.0	291.4	147.4	21.4
	Notenomouridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	Calocidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Ecnomidae	0.2	0.0	0.0	0.0	0.2	0.0	0.2	0.0
	Hydrobiosidae	0.2	2.6	0.0	0.2	1.0	1.4	0.8	17.0
	Hydroptilidae	7.2	20.0	1.0	0.8	3.4	4.2	1.8	4.6
	Leptoceridae	0.0	0.2	0.0	0.0	0.0	0.4	0.2	0.0
Tooms River Site BB									
Ephemeroptera	Baetidae	30.8	66.8	20.2	2.4	44.2	18.2	2.4	0.4
	Caenidae	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
	Leptophlebiidae	54.2	84.6	168.2	11.6	104.2	62.6	46.2	57.4
Plecoptera	Eusthenidae	2.4	7.4	15.0	2.6	17.8	7.6	8.6	8.6
	Gripopterygidae	127.2	74.6	27.4	6.2	30.8	22.8	13.4	8.4
	Notenomouridae	29.2	1.2	0.0	20.8	2.0	0.8	0.0	20.2
Trichoptera	Calocidae	6.2	15.0	11.2	1.4	14.8	2.2	1.4	1.8
	Ecnomidae	12.6	3.0	0.4	3.0	4.0	3.6	1.4	9.0
	Hydrobiosidae	5.2	16.8	16.8	1.8	4.0	5.0	0.2	1.4
	Hydroptilidae	6.0	2.0	3.0	0.8	3.2	0.2	0.0	9.2
	Leptoceridae	8.8	9.8	18.4	1.8	4.6	0.8	1.6	0.6

Table 5.8. Mean abundance of main Ephemeroptera, Plecoptera and Trichoptera (EPT) families collected per sample (n = 5) at each study site on each collection date (continued)

Collection round		1	2	3	4	5	6	7	8
Date		Jan 06	April 06	July 06	Nov 06	Mar 07	June 07	Sept 07	Nov 07
Macquarie River Site CB									
Ephemeroptera	Baetidae	9.4	0.0	0.0	0.8	5.8	0.0	0.0	0.4
	Caenidae	3.8	0.0	0.2	0.0	11.4	0.0	0.6	2.2
	Leptophlebiidae	326.0	13.0	2.2	149.0	10.0	2.6	4.4	81.8
Plecoptera	Eusthenidae	9.0	0.0	0.0	8.0	0.0	0.0	0.0	15.8
	Gripopterygidae	22.0	39.8	59.8	38.0	149.6	233.0	150.4	56.4
	Notenomouridae	21.8	0.2	0.0	6.0	1.6	0.0	0.8	48.0
Trichoptera	Calocidae	2.4	2.0	0.0	3.3	0.4	0.2	0.2	0.0
	Ecnomidae	5.8	0.2	0.0	0.0	5.0	0.0	0.0	0.8
	Hydrobiosidae	7.0	1.0	0.0	0.8	0.2	0.2	0.4	0.4
	Hydroptilidae	4.6	1.2	0.8	63.3	28.4	0.4	0.8	3.2
	Leptoceridae	3.8	0.0	0.2	0.3	5.4	0.0	0.2	2.6
Macquarie River Site IF									
Ephemeroptera	Baetidae	4.0	0.6	0.0	1.5	5.4	0.2	0.0	0.0
	Caenidae	1.8	0.0	0.4	2.0	0.6	0.6	0.2	3.2
	Leptophlebiidae	52.2	5.4	1.0	71.5	4.8	25.2	36.8	187.2
Plecoptera	Eusthenidae	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
	Gripopterygidae	1.2	10.2	11.0	3.3	12.0	23.4	5.0	6.4
	Notenomouridae	5.2	0.0	0.0	21.0	0.0	0.0	2.4	17.8
Trichoptera	Calocidae	0.4	0.0	0.4	1.0	0.4	0.0	0.0	0.2
	Ecnomidae	0.2	0.0	0.2	1.0	1.6	0.4	1.6	0.6
	Hydrobiosidae	23.2	0.8	0.0	7.3	1.2	6.4	2.4	1.0
	Hydroptilidae	1.6	0.2	0.0	6.0	10.0	2.6	5.2	2.4
	Leptoceridae	43.0	1.4	0.4	2.8	1.0	0.6	2.2	1.2

Trichoptera were patchily distributed at all sites, but were more common at BB than at the other sites. Most Trichoptera families decreased in abundance at all sites during the study period. Calocidae were most common at BB, never collected at TL and rare at IF. Leptoceridae were also rare at TL, but common at IF. Hydroptilidae were common at all sites in most collection rounds. Hydrobiosidae was the most abundant caseless caddis taxon, and more common at the two downstream sites, BB and IF.

5.4.4 Functional feeding group abundance

There were strong differences in the abundances of some functional feeding groups (FFG) at the upstream Tooms site, TL between the first collection round in January 2006 and the final collection in November 2007 (Appendix 5). Collectors ($F_{(1, 9)} = 18.947$, $p = 0.0024$) and filter feeders ($F_{(1, 9)} = 5.678$, $p = 0.044$) were significantly more abundant in 2007. Scrapers, in contrast, were significantly less abundant ($F_{(1, 9)} = 33.315$, $p = 0.0004$) in November 2007. Both scrapers ($F_{(1, 9)} = 5.407$, $p = 0.048$) and shredders ($F_{(1, 9)} = 6.806$, $p = 0.031$) were less abundant at the upstream Macquarie site, CB in November 2007 than in January 2006.

There were fewer differences in FFG abundance at the downstream sites. Filter feeders were more abundant in November 2007 ($F_{(1, 9)} = 10.172$, $p = 0.013$) at the downstream Tooms site, BB, and were the only FFG to show a significant difference. There were no significant differences in FFG abundances at the downstream Macquarie site, IF between the first and last collection rounds.

5.5 Discussion

The results of this study support McMahon and Finlayson's (2003) contention that "anti-drought" flow regimes can profoundly alter aquatic communities, even in the absence of thermal effects from hypolimnial

releases. The differences between the rivers persisted at the downstream Tooms site, BB, approximately 8 km downstream of the dam and despite the additional 1920 ML per year input from minor tributaries (CFEV 2005). While the community structure at BB was more similar to the Macquarie River sites than to TL, substantial differences remained, even before the drought intervened. For example the crustaceans Ceinidae (Amphipoda) and Uramphisopinae (Isopoda) were absent from BB, but Sialidae (Megaloptera) and Athericidae (Diptera) were present at this site, but not at the Macquarie sites.

As observed in several comparative studies of river regulation (Fig. 5.1) the invertebrate fauna directly below the Tooms Lake dam (TL) was depauperate, and dominated by snails, chironomids and mites. Similar results were found below deep release dams on the Cotter River in the ACT (Nichols *et al.* 2006), in Colorado (Voelz and Ward 1989) and in Portugal (Miserendino 2009). In addition, there were fewer low flow specialists and fewer EPT taxa, as predicted by Poff *et al.* (2010).

The impact of the drought on the unregulated Macquarie River was consistent with the general patterns documented in similar river systems (Figure 5.2, Table 5.1). Rheophilic taxa, such as Leptophlebiidae and Elmidae, decreased in abundance, as did other scraper-grazers (e.g. Hydrobiidae). The shredding amphipod, Ceinidae, also decreased in abundance, in line with the reduction in organic material with the drought (Bogan and Lytle 2007). Contrary to expectations, the fauna in the regulated Tooms River remained distinct in the latter stages of the drought, despite the negligible flow regime. Whereas strong dispersers, such as Dytiscidae and Odonata were expected to colonise Tooms River with the reduction in flow, Dytiscidae remained rare, and *Austroaeschna unicornis* (Telephlebiidae) was the only Odonata taxon common in Tooms River at any time. It was surprising that Zygoptera, which were common in pools at the

downstream Macquarie site, IF, did not colonise the downstream Tooms site, BB.

It is apparent that the long-term changes to the macroinvertebrate fauna wrought by the anti-drought flow regime can persist, even through 2 years of a supra-seasonal drought, and with the close proximity of source populations in remnant pools in the Macquarie River. In addition, the high benthic biofilm mass, stimulated by the higher nutrient concentrations in Tooms River (Table 4.8) is likely to have discouraged colonisation by those taxa which require clean rock surfaces and clear water (Nichols *et al.* 2006).

5.5.1 Regulation effects on faunal communities

The effect of flow regulation was most apparent when comparing the Macquarie River sites with the upstream Tooms site, TL. Diversity was much lower at TL (Fig. 5.3), and many taxa recorded at the other 3 sites were absent. However, some taxa which were seasonally abundant in remnant pools in the Macquarie (e.g. such as the crustacean *Paratya australiensis* (Atyidae) and most Hemiptera) were absent from both Tooms sites (Appendix 4).

The taxa dominant at TL were generally those which are common in other regulated river studies (e.g. Nichols *et al.* 2006), (i.e. molluscs, nematodes and mites). The abundance of snails and mites was several orders of magnitude higher at TL than at the Macquarie sites, or at the downstream Tooms site, BB. However, there were some differences from other studies, potentially due to the absence of thermal effects, which confound many studies of river regulation. This is difficult to quantify because many studies do not specify the reservoir depth or the water release method (e.g. Takao *et al.* 2007; Boix *et al.* 2010).

Gripopterygidae (primarily *Leptoperla varia* and *Dinotoperla* sp.) were more abundant at TL than at any other site and were 3 times as

abundant at TL as at the downstream Tooms site, BB. By contrast, Plecoptera were absent from regulated sites on the Nepean-Hawkesbury River system (Growns and Growns 2001) and below the Dworshak Dam in Idaho (Munn and Brusven 1991). Simuliidae were also abundant at TL, but this taxon has been reported as responding positively to regulation in some studies (e.g. Voelz and Ward 1989; Takao *et al.* 2007; Reich *et al.* 2009), but negatively in others (e.g. Nichols *et al.* 2006). These studies are all of deep release dams, which suggests that the presence or absence of Simuliidae may be related to some factor other than stream temperature, particularly as the abundance of this taxon was low at the downstream Tooms site, BB. For example, several studies (e.g. Carlsson *et al.* 1977; Brittain and L'Abée-Lund 1995) have recorded high abundances of Simuliids feeding on seston and zooplankton released from lake outlets.

The ephemeropterans Leptophlebiidae and Baetidae, and the coleopterans Psephenidae and Dytiscidae, were rarely collected at TL. Few Leptophlebiidae were found in regulated branches of the Mitta Mitta River in Victoria (Pardo *et al.* 1989), or in North American and Spanish regulated streams (Ward and Garcia de Jalón 1991). Several studies have recorded low Baetidae abundance below dams (e.g. Pardo *et al.* 1989; Camargo and Voelz 1998; Nichols *et al.* 2006). Reich *et al.* (2009) attributed the abundance of Baetidae in regulated streams of the Broken-Boosey Creek system in Victoria to the more reliable flow regime than in their intermittent unregulated streams. Hydropsychidae (Trichoptera) were also more abundant in their regulated streams. Baetidae and Hydropsychidae were indicator taxa for the downstream Tooms site, BB, but were rare at the upstream Tooms site, TL, suggesting that these taxa may be benefiting from the more reliable flow regime at site BB, in a similar manner to that suggested by Reich *et al.* (2009), but that benthic conditions (i.e. smothering of the stream bed in thick biofilms) may prevent these taxa from surviving at TL. Notably, different Baetidae species are found across a broad range of conditions

(Reich *et al.* 2009) and greater taxonomic resolution is needed for this family to properly understand the responses to flow regulation.

5.5.2 Recovery of faunal communities with distance from the dam

Several studies have recorded recovery of the invertebrate community to near pre-impoundment condition with distance from a dam (e.g. Voelz and Ward 1989; Petts *et al.* 1993; Nichols *et al.* 2006), but invertebrate family diversity remained lower, on average, at the downstream Tooms site, BB than at the Macquarie sites (Fig. 5.3), mainly due to the absence of seasonal variation in invertebrate community composition.

The increased diversity below dams is frequently linked to input from minor tributaries, as shown below the Canning Dam in Western Australia (Storey *et al.* 1991), the Yahagi dam in Japan (Takao *et al.* 2007) and the Dworshak Dam in Idaho (Munn and Brusven 1991). On this basis, the input from minor tributaries was expected to contribute to the recovery of the invertebrate community at the downstream Tooms site, BB. Indeed, some taxa which were absent from TL were at least as abundant at BB as at the Macquarie sites (e.g. Psephenidae, Elmidae Leptophlebiidae, Baetidae, Empididae, Ceratopogonidae, Leptoceridae, Calocidae, Ecnomidae and Philorheithridae (see Appendix 4).

However, there were other taxa which were unexpectedly absent from BB. For example, *Paratya australiensis,* which Reich *et al.* (2009) found below several dams on the Broken-Boosey Creek system in Victoria, was absent from both Tooms River sites. The scarcity of vascular macrophytes at BB may have influenced this, because *P. australiensis* was only found in pools with macrophytes at the Macquarie sites. Vinson (2001) predicted that amphipods would be disadvantaged in rivers with turbid water and few macrophytes, which makes the abundance of amphipods (*Austrochiltonia* sp.: Ceinidae) at TL surprising, although Grown and Growns (2001) contended that amphipods would positively respond to flow regulation. In contrast to

Voelz and Ward's (1989) suggestion that shredders would increase as leaf litter increased downstream of a dam, amphipods were rare at BB, but abundant at all the other sites, despite the abundance of leafy detritus at BB (Chapter 4).

Of the collector-scrapers, Baetidae and Leptophlebiidae were both more abundant at BB than at TL, whereas filter feeders (Simuliidae) were less abundant at BB. Camargo and Voelz (1998) found similar patterns for Leptophlebiidae and Simuliidae in their study, but the converse for Baetidae. They attributed this to inputs from warmer tributaries in their Colorado sites, whereas rapid flow fluctuations below a Spanish hydro-electric storage eliminated Leptophlebiidae while increasing densities of Baetidae and Simuliidae. However, thermal effects and rapid flow fluctuations were absent from Tooms River, which suggests that different factors influence Simuliidae abundance to those that influence Baetidae or Leptophlebiidae abundance.

Elmidae and Hydropsychidae became more abundant downstream of both the Colorado and Spanish dams (Camargo and Voelz 1998). This also occurred in Tooms River, which seems to indicate that a common regulation factor influences the abundance of these taxa, despite the differences in flow and thermal regimes between the three regulated rivers. Camargo *et al.* (1998) suggested that scraper-grazers would increase in abundance with distance from the dam, because sediment deposition immediately below dams could favour deposit feeders at the expense of scrapers (Armitage 1987). However, this prediction was only realised for Psephenidae in Tooms River, while mollusc abundance decreased with distance from Tooms Lake.

5.5.3 Faunal differences between the Macquarie sites

There were also some strong differences between the Macquarie River sites (Appendix i, Appendix 4). Both Macquarie sites developed a pool community in summer, but mobile neustonic/nektonic hemipterans,

such as *Rheumatometra philarete* (Gerridae) and *Sigara australis* (Corixidae), were only found at the upstream site, CB, while Culicidae and tadpoles characterised the downstream site, IF. The absence of hemipteran taxa from the downstream site was unlikely to be due to differential predation pressure, because predatory fish were found in pools at both sites.

Large-bodied, long-lived species, such as *Eusthenia spectabilis* (Eusthenidae: Plecoptera) (Hynes and Hynes 1975) and *Sclerocyphon aquaticus* (Psephenidae) (Davis 1998), were present at CB and at BB, but absent from the downstream Macquarie site, IF. *Synthemiopsis* sp. (Synthemistidae: Odonata) were common at IF, but not at CB. This taxon would be suited to the shallow pools and abundant macrophytes at IF (Gooderham and Tsyrlin 2002). While there were permanent pools upstream and downstream of IF to provide recolonising insects, this study reach completely dried out in summer. Accordingly, the species found at this site were those which are able to survive in shallow permanent pools upstream or downstream of the study site, such as *Triplectides* spp. (Trichoptera: Leptoceridae), or with short life cycles (e.g. Chydoridae (Cladocera) and Ostracoda) (Gooderham and Tsyrlin 2002).

However, Cladocera and Ostracoda were also common at the upstream Tooms site, TL, and it is likely that different species dominate in these contrasting sites. Chironomids, simuliids and nematodes were also more abundant at IF and TL than at CB or BB, which suggests that the broadwater pool upstream of IF is influencing the species abundance at this site. However, there were some taxa, such as Elmidae and Leptoceridae, which were most abundant at IF and BB, the downstream Tooms site, which may relate to the proximity of these sites.

5.5.4 The temporal changes due to drought in the unregulated Macquarie River

Both Macquarie River sites dried to disconnected pools during the drought. Rheophilic taxa, such as Elmidae, Leptophlebiidae, and Baetidae (*Centroptilum* sp.) decreased in abundance, as predicted by Boulton (2003). Bond *et al.* (2008) suggested that scrapers would be stranded by falling water levels. Hydrobiidae and Psephenidae were abundant in the first collection round, but became rare as the drought progressed. Surprisingly, the abundance of seasonal lentic taxa, such as Corixidae and Gerridae, also decreased at the upstream site, CB, possibly because overwintering refugia dried out (Bogan and Lytle 2007). However tolerant taxa, such as Chironomidae, also declined, although this may have been due to predation pressure in shrinking pools (Fig. 5.2). Boix *et al.* (2010) found that Chironomidae increased in abundance with drought in one unregulated Spanish river, where there was abundant filamentous algae, but decreased in a second river, where algae were less prominent, which suggests that low flows may not be the only factor influencing chironomid abundances during a drought.

5.5.5 The temporal changes due to drought in the regulated Tooms River

It was hypothesised that drought would allow establishment of some mobile, lentic taxa in Tooms River, so that the fauna of Tooms River and the Macquarie River would converge on a similar community structure, dominated by slow flow specialists. However, the lentic taxa which seasonally characterised the Macquarie sites did not colonise either Tooms site. The communities of Tooms River became less similar to the Macquarie sites, with the strongest effects at the upstream site, TL. Whereas molluscs dominated the communities at TL in the first collection round, chironomids, copepods, simuliids and mites were more abundant than molluscs in the final round.

Gripopterygidae, the main indicator for the unregulated sites (Table 5.5) and Leptophlebiidae decreased in abundance, while Baetidae were completely absent from the final round. No Ephemeroptera were collected in the final round at TL. Shredding taxa, such as the Trichoptera families Leptoceridae and Calocidae, were abundant at BB in the early rounds, but became rare with the reduction in channel width and reduced access to leaf litter. The shredding amphipod, Ceinidae, while always rare at BB, also became rare at TL. However, predatory taxa, such as Eusthenidae and Ecnomidae became more abundant under drought condition, as Boulton and Lake (1992b) predicted, with prey concentrated into a smaller area.

While rheophilic taxa decreased in abundance in both rivers, Tooms River did not develop the lentic taxa or seasonal variation that characterised the Macquarie sites. Moreover, the drought had a severe impact on the invertebrate fauna of Tooms River, particularly at the upstream site, which supports McMahon and Finlayson's (2003) proposal that the loss of extreme low flows and cease-to flow periods of the anti-drought flow regime in Tooms River would have a greater effect on the invertebrate communities than natural disturbance in an unregulated river.

5.5.6 Limitations of assessing regulation effects from invertebrate community composition

The presence or absence of an aquatic invertebrate species at a particular location is a function of the flow regime, but also such factors as habitat and resource availability, both of which are also influenced by the flow regime (Hynes 1970a; Petts 1984).

The abundance of some taxa generally complied with other studies of regulated rivers (e.g. snails and mites), but there were inexplicable differences in the presence or absence of some other taxa. For example, Gripopterygidae were very abundant near the Tooms Lake dam, but less

abundant downstream, and not found in some other regulated rivers (e.g. Munn and Brusven 1991; Growns and Growns 2001). Ceinidae were also abundant at every site except the downstream Tooms site, BB. While the absence of lentic taxa from Tooms River could be attributed to the rarity of low flows, there was no apparent reason why one leptocerid species, *Lectrides varians*, a common shredder in the Macquarie River, should be missing from BB, when there were several other Leptoceridae common to both rivers.

There have been several attempts to predict invertebrate community composition based on species traits (e.g. Growns and Davis 1994; Townsend and Hildrew 1994). However, using this approach to assess the complex effects of flow regulation has limitations. For example, there were few taxa which fitted Growns and Davis (1994) classification of flow obligates in either the Macquarie or Tooms River (Appendix 4). Many of these (e.g. Athericidae) were most abundant at the downstream Tooms site, despite the close similarity in the flow regime to the upstream Tooms site. Several taxa classified as flow avoiders were also more abundant in Tooms River, but these tended to be tolerant taxa which graze on biofilms (e.g. Physidae).

5.6 Conclusion

The anti-drought flow regime in Tooms River has had large effects on the invertebrate communities, which persisted through and were exacerbated by the supra-seasonal drought. Many of the invertebrate responses to regulation of Tooms River have been documented elsewhere, while some of the different responses can be attributed to thermal effects or the confounding influence of land use (e.g. Reich *et al.* 2009). However, there were some surprising deviations from expectations, such as the high abundance of Gripopterygidae at the upstream Tooms site.

Some of the phenomena predicted in Figure 5.1 were supported. Diversity was lower, and grazers, amphipods and tolerant taxa (e.g. chironomids and gastropods) were more abundant at the upstream site. However, collector-gatherers and filter feeders were less abundant than expected. Oligochaetes were more important at the downstream site, and rheophilic taxa were abundant before the drought took hold. Taxa considered sensitive to poor water quality (Chessman 2001, 2003), such as Gripopterygidae, were unexpectedly abundant at TL, while equally sensitive Leptophlebiidae and Eusthenidae were abundant at the downstream Tooms site, but not at TL. Microcrustaceans were a prominent component of the fauna at TL, as expected, but were also common at the downstream Macquarie site, IF.

There were, however, some prominent discrepancies with other studies. For example, amphipods and other crustaceans were rare at the downstream Tooms site. Some trichopteran taxa were unexpectedly missing, while other taxa, such as Athericidae and Sialidae, were only found at BB. Some of these discrepancies could be due to the coarse taxonomic resolution used both here and in other studies (e.g. Baetidae, some trichopteran families), and some critical evaluation of which taxa may merit finer taxonomic resolution is warranted in future studies of flow regulation and drought. In addition, invertebrate dispersal needs closer attention. There were some surprising absences or reduced densities of some taxa in the lower Macquarie site, as well as the Tooms sites, despite the close proximity of sources of colonists in the Macquarie. Future studies combining population genetics with direct field observations would help identify whether these patterns were due to differences in dispersal ability or differential post-dispersal processes (e.g. recruitment, or species sorting via competition or predation). Better understanding of these processes is needed before progress can be made in assessing the potential for regulated river reaches to be restored or rehabilitated

Petts (1980) proposed a three stage assessment of the effects of flow regulation. The results of this study support his suggestion that the 1st-order impacts of the altered hydrological regime and resultant 2nd-order effects on the channel form, the riparian vegetation and the availability of resources would produce 3rd-order impacts on the aquatic fauna. What this assessment does not determine, however, is which aspects of the 2nd-order effects have the strongest influence on aquatic communities. The ELOHA framework (Poff *et al.* 2010) attempts to resolve this impasse, by defining ecologically meaningful characteristics for each river segment, based on hydraulic habitat features and responses of biotic variables to variations in flow. The ecological classification can then be tested with field sampling, targeted to resolving specific questions. This framework has the potential to resolve some of the anomalies in the Tooms and Macquarie River macroinvertebrate data, particularly as conditions in these rivers are not limited by the confounding thermal or land use effects, which restrict most studies of this type (Poff *et al.* 2010).

Implementation of this framework is, however, impeded in Australia because of our more limited database on the flow requirements of many of our taxa. There is currently no equivalent to North American and European "trait-based" classifications of benthic taxa, which is a deficiency that needs to be redressed.

Additional research is also needed into the long-term consequences of drought for aquatic biota, particularly with climate change forecast to increase the frequency and duration of drought in some areas (Grose *et al.* 2010). This study has shown that the invertebrates in the Macquarie River are more resistant to drought than those in Tooms River. However, to assess the resilience of these invertebrate taxa, post-drought sampling needs to continue for a much longer time period than the short-term focus of most studies, and allow for time-lags in the response of specific species to supra-seasonal droughts (Lake 2000).

Appendix i: Macroinvertebrate indicator taxa for each study site

Indicator values and probability of that macroinvertebrate taxon being indicative of variation between the Tooms River sites (TL and BB)

Taxon	Site	Indicator value	Probability
Physidae	TL	0.627	0.001
Ancylidae	TL	0.563	0.001
Nematoda	TL	0.492	0.001
Copepoda	TL	0.471	0.001
Glacidorbidae	TL	0.410	0.001
Acarina	TL	0.405	0.001
Gripopterygidae	TL	0.344	0.004
Turbellaria	TL	0.235	0.006
Psephenidae	BB	0.536	0.001
Athericidae	BB	0.499	0.001
Calocidae	BB	0.471	0.001
Baetidae	BB	0.463	0.001
Eustheniidae	BB	0.454	0.001
Sialidae	BB	0.376	0.001
Empididae	BB	0.374	0.001
Leptophlebiidae	BB	0.362	0.001
Ecnomidae	BB	0.345	0.001
Ceratopogonidae	BB	0.334	0.001
Hydrobiosidae	BB	0.306	0.001
Elmidae	BB	0.298	0.001
Leptoceridae	BB	0.267	0.009
Philorheithridae	BB	0.261	0.001
Tanyderidae	BB	0.214	0.026
Notonemouridae	BB	0.211	0.011
Atriplectididae	BB	0.189	0.001
Hydropsychidae	BB	0.127	0.019
Conoesucidae	BB	0.066	0.049

Indicator values and probability of that macroinvertebrate taxon being indicative of variation between the Macquarie River sites (CB and IF).

Taxon	Site	Indicator value	Probability
Ceinidae	CB	0.480	0.001
Uramphisopinae	CB	0.381	0.001
Janiridae	CB	0.259	0.001
Scirtidae	CB	0.222	0.004
Dytiscidae	CB	0.191	0.002
Sphaeridae	CB	0.180	0.007
Corixidae	CB	0.148	0.001
Atyidae	CB	0.137	0.011
Gerridae	CB	0.093	0.017
Ostracoda	IF	0.400	0.001
Tanypodinae	IF	0.328	0.003
Chydoridae	IF	0.287	0.001
Synthemistidae	IF	0.162	0.001
Sisyridae	IF	0.103	0.009
Vellidae	IF	0.092	0.009
Culicidae	IF	0.092	0.023

Chapter 6 The importance of allochthonous and autochthonous resources to the macroinvertebrate food webs.

This chapter investigates the use of the available benthic resources by macroinvertebrates and is comprised of two sections, which have been submitted for publication to two different journals. There is some duplication of information from earlier chapters, particularly in the Methods sections, due to the requirements of the individual journals. References cited in this chapter have been incorporated into the *Bibliography.* Details of authors, publication status, and the journals to which the manuscripts have been submitted are provided at the beginning of each section.

Triplectides similis (Trichoptera: Leptoceridae) in case made of woody vegetation, feeding on *Myriophyllum salsugineum* frond.

6.1 Stable isotope analysis of riverine food webs

Watson, A. and Barmuta, L.A., Stable isotope analyses demonstrate that long-term river regulation results in unexpected shifts in food webs. *Freshwater Biology* (in review).

6.1.1 Abstract

1. Regulation of the flow regime is likely to affect the availability of resources for aquatic biota, although few studies report on the effect of river regulation on benthic macroinvertebrate food webs. Tooms River in eastern Tasmania, Australia, was dammed in 1840, with consequent changes to the stream channel, riparian vegetation and resource availability.

2. We used stable carbon and nitrogen isotope analyses to examine the use of available food resources by benthic macroinvertebrates in the regulated Tooms River and the adjacent unregulated Macquarie River. Terrestrial leaf litter was abundant in both rivers and was expected to be an important food resource.

3. Unexpectedly, invertebrates in the regulated river were significantly more $\delta^{13}C$ enriched than those in the unregulated river, in contrast to most published regulated river studies.

4. Invertebrate stable isotope signatures in the regulated river were dominated by algae and cyanobacteria. Isotope signatures in the unregulated river were dominated by emergent macrophytes, a controversial result which was confirmed with feeding preference trials.

5. This demonstrates that even small dams can alter the flow regime sufficiently to impact on riverine food webs. A similar long-term shift in the resource base is likely to occur in other regulated streams in Mediterranean climate zones, as irrigation dams mature.

6.1.2 Introduction

Few studies examine the effects of river regulation on the use of food resources by benthic aquatic macroinvertebrates, with most studies focussed on fish or water birds (e.g. Benstead *et al.* 1999). Regulation of rivers for irrigation in temperate climates usually results in a reversal of flow seasonality (Arthington and Pusey 2003). High flows tend to be in the dry season, with lower flows prevailing in the wet season (McMahon and Finlayson 2003). Most studies also focus on larger impoundments where the thermal stratification of the reservoir during the dry season confounds the flow effects of irrigation releases (e.g. Chester and Norris 2006). There is little published on the effects of smaller reservoirs that do not stratify, and such impoundments are likely to be more numerous than large reservoirs. In addition, the reversed seasonality of irrigation releases in Mediterranean climate zones are likely to have different impacts on ecosystem processes than releases from hydro-electric power or flood mitigation reservoirs.

Stable isotopes are commonly used to investigate food webs. The symbol $\delta^{13}C$ expresses the relative per mille ratio of the stable carbon isotopes, ^{12}C and ^{13}C, against the international standard Pee Dee belemnite (Craig 1957). This differs sufficiently in plants and algae to provide insight into the assimilation of resources into food webs. Carbon stable isotope ratios vary less than 0.1‰ between animal tissues and the food they consume (DeNiro and Epstein 1978; McCutchan *et al.* 2003). The trophic enrichment, or fractionation, of $\delta^{15}N$, the ratio of the stable nitrogen isotopes ^{14}N and ^{15}N against the standard (atmospheric nitrogen) has been calculated as 2.6‰ -3.4‰ (DeNiro and Epstein 1978; Minagawa and Wada 1984; Peterson and Fry 1987). However, the level of fractionation can be variable and influenced by the environment and diet of the consumer (Vander Zanden and Rasmussen 2001; McCutchan *et al.* 2003).

Of the published studies on rivers regulated for irrigation, $\delta^{13}C$ depletion and $\delta^{15}N$ enrichment characterised invertebrates in an Australian Capital Territory river (Chester and Norris 2006) and periphyton in the Murrumbidgee River system (Chessman *et al.* 2009b) relative to nearby unregulated streams. River regulation has shifted the resource base in the Murray River, SE Australia, from heterotrophic bacteria to less nutritious filamentous green algae (Sheldon and Walker 1997), while autochthonous resources also dominated the food web below low navigation control dams in the Ohio River, USA (Thorp *et al.* 1998; Pomeroy *et al.* 2000). Several studies of the effects of large hydro-electric dams on the Colorado River (e.g. Angradi 1994; Pomeroy *et al.* 2000; Vinson 2001) also report $\delta^{13}C$ depletion immediately downstream, where filamentous green algae dominates the food web. Shannon *et al.* (2001) reported that $\delta^{13}C$ became less depleted with distance downstream of the dams.

We sought to test this pattern of $\delta^{13}C$ depletion immediately downstream of a dam, followed by recovery downstream, by comparing a site below the shallow dam on Tooms River in Tasmania with a site further downstream near its confluence with the unregulated branch of the Macquarie River, and with a pair of sites on the unregulated Macquarie. A long history of regulation in the Tooms River (since 1840) has resulted in a more stable flow regime with reversed seasonality, as is typical of irrigation storages (Arthington and Pusey 2003). We anticipated that the Tooms sites may deviate from other studies because flow regulation has promoted the growth of riparian trees which overhang the river channel, potentially increasing leafy detritus, but reducing photosynthetic algal biomass. In contrast, the naturally highly variable flow regime of the Macquarie River has resulted in a distinct, shrubby riparian zone, with less obvious standing stocks of leafy terrestrial detritus and conspicuous algal and macrophyte growth during summer low flows. Leafy detritus was expected to make a substantial contribution to invertebrate diets in both rivers, as has been

observed in many temperate stream studies (e.g. Rounick *et al.* 1982; Reid *et al.* 2008; Leberfinger *et al.* 2011) although Reid *et al.* (2008) also noted the role of biofilms in riverine food webs.

The overall aim of the study was to examine the importance of leafy detritus and biofilms to the invertebrate food web, in response to the changes to the riparian vegetation resulting from 170 years of river regulation.

6.1.3 Methods

Macroinvertebrates and potential food sources were collected from two sites on each of the unregulated Macquarie River and its regulated tributary, Tooms River, 3rd order (at 1: 25 000 scale) streams in eastern Tasmania, Australia (Table 6.1.1).

Table 6.1.1 Characteristics of the study sites on the unregulated Macquarie and regulated Tooms Rivers.

River	Site	Latitude	Longitude	Catchment (km^2)	Alt (m)	Mean bankful width (m)
Macquarie	Upstream	42°09'03"S	147°49'59"E	85.9	408	8.9
	Downstream	42°09'51"S	147°42'44"E	169.3	290	5.1
Tooms	Upstream	42°12'42"S	147°46'18"E	62.5	448	2.8
	Downstream	42°11'24"S	147°43'12"E	74.2	280	5.5

The Macquarie River system shares many of the characteristics of southeast Australian rivers, including high seasonal variability and intermittent flow (Lake *et al.* 1985), while Tooms River exhibits a stable flow regime and reversed flow seasonality (Fig. 6.1.1). The region has a mean annual rainfall of about 500 mm, but had less than 380 mm per year during the study period, the lowest on record (Bureau of

Meteorology 2010). Water is released from Tooms Lake, via a gate at the base of the 4 m high dam wall, into Tooms River to augment low flows in the Macquarie River, which supplies water for downstream irrigators and domestic supply. In addition, an environmental flow requirement of 4.1 ML.day^{-1} 50 km further downstream in the Macquarie River (DPIW 2008) maintains continuous flow in Tooms River when the upper Macquarie is dry.

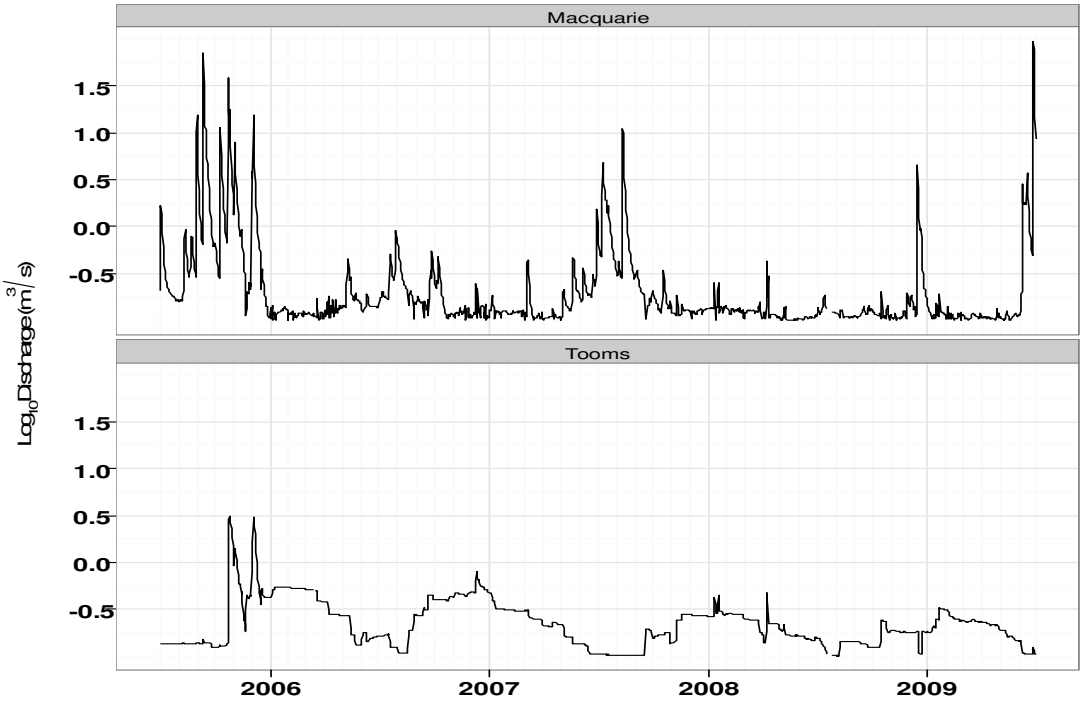


Fig. 6.1.1 Variation in mean daily discharge for the unregulated Macquarie River (upper panel) and regulated Tooms River (lower panel) from1 July 2005 – 30 June 2009, with the height of the bars indicating discharge ($m^3.sec^{-1}$) on a logarithmic (base 10) scale and date (year) on the x-axis.

Tooms Lake has a mean depth of 3.6 m and area of 6 km^2, with naturally high turbidity (Croome and Tyler 1972). Wind action on the lake suspends sediments leading to high turbidity in Tooms River (mean 26.05 NTU, maximum 106.0 NTU, 2005 – 2009) (WIST 2010) and resuspended nutrients contribute to algal and cyanobacterial blooms in the lake itself.

The study sites were comparable between rivers in terms of geology and land use. All sites had confined channels and bedrock controlled cobble and boulder substrates. A shallow bridge constricted the flow above the downstream Macquarie site, resulting in a narrower and deeper channel than that at the upstream site. Both upstream sites were surrounded by natural open *Eucalyptus* spp. woodland, with a distinct riparian zone at the Macquarie River sites, dominated by sclerophyllous *Leptospermum* and *Acacia* shrub species. The riparian zone was less distinct at the regulated Tooms River sites, where mature eucalypt trees extended to the water line. Plants typical of higher rainfall areas, such as ferns and mosses, dominated the understorey at the site nearest the dam. The riparian zones at the downstream sites were essentially natural open woodland, but both sites were surrounded by land cleared for low-intensity (< $0.5.ha^{-1}$) sheep grazing.

The study commenced in December 2006, with samples collected quarterly to examine seasonal differences in resource availability, until January 2008, when there was no flow in the Macquarie River (hereafter 'Macquarie'). No invertebrates were collected from Tooms River (hereafter 'Tooms') in autumn 2007, due to a persistent cyanobacterial bloom, or from the completely dry downstream site on the Macquarie in January 2008. Invertebrates were collected from remnant pools at the upstream Macquarie site during most of this period. A final collection was made from both the Macquarie sites in January 2009 after flow returned. The Tooms sites were not sampled in 2009 because there had been no substantial flows during the previous year and it was not possible to collect sufficient invertebrates for analysis.

On each occasion, two operators collected benthic invertebrates with a kick net and by hand picking from leaf packs, stones and woody debris, over a 1.5 - 2 hour period. Live invertebrates were maintained in filtered river water for at least 24 h to void gut contents, with individual Trichoptera placed in separate containers to prevent case consumption.

Conditioned leaves and leaves of vascular macrophytes were collected from the river beds and banks. Biofilms were sampled by collecting whole rocks, which were transported on ice, in sealed bags of stream water, to the laboratory.

After freezing, invertebrates were cleaned of attached algae under a dissecting microscope, dried (48 h, 40° C), then ground to a fine powder with a glass mortar and pestle. Biofilms, protozoan and *Nostoc* colonies were scraped from rocks with a scalpel blade and foreign material removed under a dissecting microscope. Samples of pelagic algae were obtained by colloidal silica density fractionation of concentrated river water (Hamilton *et al.* 2005). All plant and algal samples were rinsed with distilled water before drying (48 h, 40° C) and grinding with a mortar and pestle.

Stable isotope ratios and percentage carbon and nitrogen were measured on a 20/20 continuous flow isotope analyser (Europa Scientific, Inc., Franklin, Ohio, USA) at the Stable Isotope Unit at Waikato University, Hamilton, New Zealand. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as parts per thousand (‰) difference between the samples and conventional standards (CSIRO sucrose, with a $\delta^{13}C$ of -10.80‰, traceable to Pee Dee belemnite, and $\delta^{15}N$ to urea at -0.499‰, standardised against atmospheric N_2).

Food sources with overlapping signatures were grouped for analysis (Phillips *et al.* 2005) as shown in Table 6.1.2, with the source codes used in the following figures. Because analysis of variance showed that there was no significant difference in carbon isotope values of the food source groups between the two rivers (all $p > 0.5$), the values were combined across all sites for all subsequent analyses.

Table 6.1.2 Food source groupings (and codes) for stable isotope mixing model analyses, with mean δ^{13} C and δ^{15} N values for each group ± 1 standard deviation. The number of samples (n) tested in each group is given in parentheses.

Group	Description	Mean δ^{13} C	Mean δ^{15} N
Algae (A, algae)	Benthic diatoms, charophytes, biofilms, floating algal mats (n = 8)	-25.99 ± 1.36	2.67 ± 1.37
Cyanobacteria (C, cyano)	Cyanobacteria, primarily *Nostoc* colonies (n = 8)	-13.06 ± 0.37	0.63 ± 1.95
Emergent macrophytes (M, macro)	Emergent aquatic plants, assimilating atmospheric CO_2 (n = 12)	-29.11 ± 1.61	3.08 ± 1.58
Submerged macrophytes (S, submacro)	Submerged aquatic plants, assimilating CO_2 or HCO_3^- (n = 10)	-23.65 ± 0.98	3.39 ± 0.95
Terrestrial (T, terr)	Terrestrial C_3 plants (n = 51)	-29.06 ± 0.82	-1.52 ± 1.31

Macroinvertebrates were aggregated into functional feeding groups (collector-gatherers - hereafter "collectors"; filterers; predators; scrapers; and shredders) before analysis (Finlay 2001) according to published Australian references (Chessman 1986; Growns and Davis 1994; Gooderham and Tsyrlin 2002), and augmented by local observations where necessary. Scrapers were further divided into coleopterans (Psephenidae and Elmidae) and Gastropoda, because gastropod δ^{13}C signatures were significantly less depleted than those of the Coleoptera ($t_{(20)}$ 5.729, $p < 0.001$). A small number of taxa were encountered sporadically and only at the Macquarie sites - there were some nektonic and pneustonic predators, some larval Nymphulinae (Lepidoptera: Crambidae) and the epibenthic *Paratya australiensis* Kemp (Decapoda: Atyidae). These were excluded from these analyses because comparisons between regulated and unregulated sites were impossible, but stable isotope values have been presented for Nymphulinae and *Paratya* to allow comparisons with values recorded in similar rivers elsewhere.

Differences in feeding group isotope values between rivers, sites and seasons were tested with one-way analysis of variance (ANOVA). Post-

hoc Tukey – Kramer multiple comparison tests identified which sites were different when a significant effect was detected. The SIAR (Stable Isotope Analysis in R: Parnell and Jackson 2008) package (version 4) under R 2.11.2 (R Development Core Team 2010) assessed the proportional contribution of the different food sources to each feeding group. This produced a Gaussian likelihood of diet by fitting a Bayesian model, via 200 000 Markov Chain Monte Carlo simulations, to Dirichlet prior-distributed food source values (Parnell and Jackson 2008). SIAR incorporates variation in the values of food sources, generating density plots of credible intervals for the estimated parameter (Parnell and Jackson 2008; Parnell *et al.* 2010). This procedure has been used in other recent analyses of stable isotopes in freshwater food webs (e.g. Giling *et al.* 2009; Bond and Diamond 2011). Credible intervals indicate posterior probability estimates (Edwards *et al.* 1963) and can be interpreted as Bayesian confidence intervals (Lee 1997). Carbon and nitrogen concentrations were incorporated in the model to down-weight the effect of high nitrogen values in some sources (Phillips and Koch 2002). We did not correct for carbon or nitrogen trophic fractionation in the model, because the trophic positions of the invertebrates in this study were unknown and introducing a fixed fractionation value could lead to erroneous results (McCutchan *et al.* 2003).

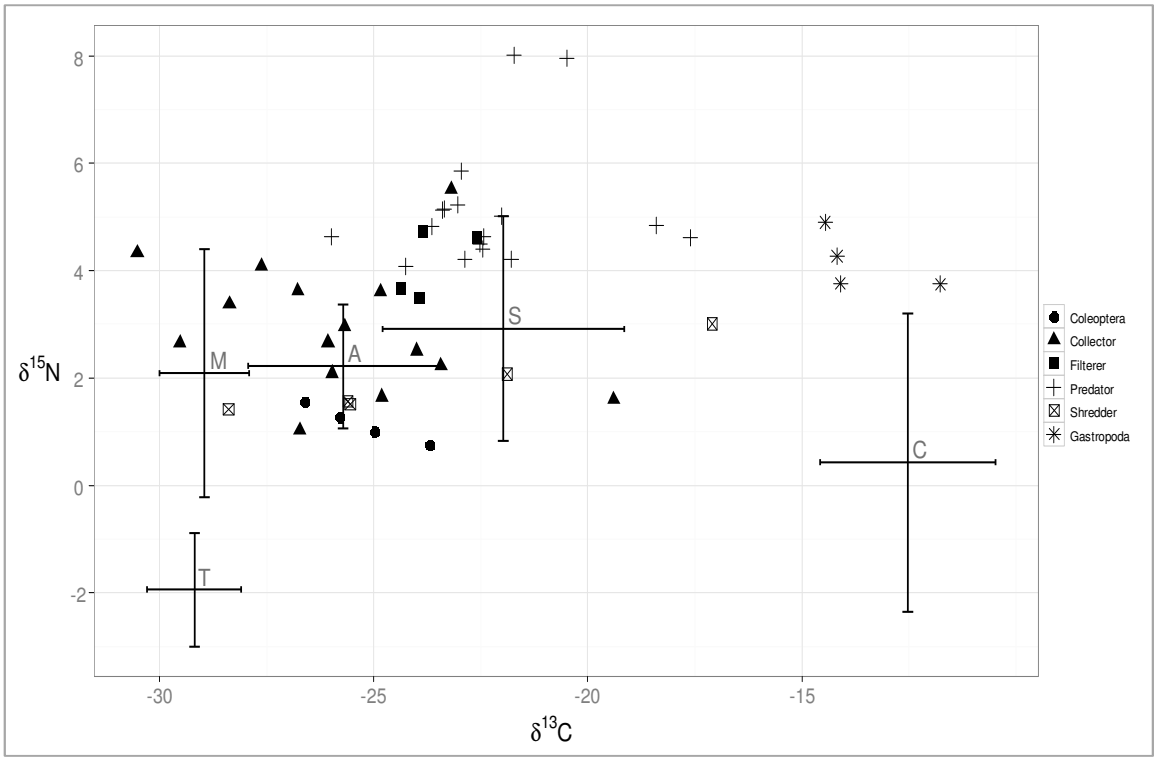
Because stable isotope signatures can be influenced by variation in nutrient concentrations in the environment (Peterson and Fry 1987), soluble nutrients in the water column were assessed by collecting 100 mL water samples in acid-washed bottles from each site when sampling for other variables. Samples were transported on ice to the laboratory and frozen (-18^{o} C) until analysis for total organic carbon, and total dissolved nitrogen and phosphorus by APHA method 4500, at the NATA accredited Analytical Services Tas laboratory at New Town, Tasmania. Additional nutrient data for Tooms River were taken from a quarterly water quality monitoring programme undertaken by the Tasmanian Department of Primary Industries, Parks, Water and Environment

(WIST 2010). Analysis of variance was used to test for significant differences between sites or rivers.

6.1.4 Results

The patterns of $\delta^{13}C$ depletion were the reverse of those found by other studies of food webs in regulated rivers. There were substantial differences between the regulated and unregulated rivers, with all invertebrates except gastropods from the regulated river significantly less $\delta^{13}C$ depleted than invertebrates from the unregulated river (Fig. 6.2, Table 6.1.3). Collectors, shredders and predators had a significantly higher $\delta^{13}C$ at the upstream Tooms site than at the downstream Tooms site, but there was no significant difference between upstream and downstream sites on the Macquarie River. However, the differences between the rivers and sites were not based on differences in the carbon isotope signatures of the food sources, which did not differ significantly between rivers or sites (all $p > 0.5$).

Cyanobacteria were the least $\delta^{13}C$ depleted food source, while algal $\delta^{13}C$ signatures were intermediate between submerged macrophytes and emergent macrophytes. Terrestrial resource $\delta^{13}C$ values overlapped emergent macrophyte signatures, but could be differentiated on the basis of $\delta^{15}N$ values (Table 6.1.4).



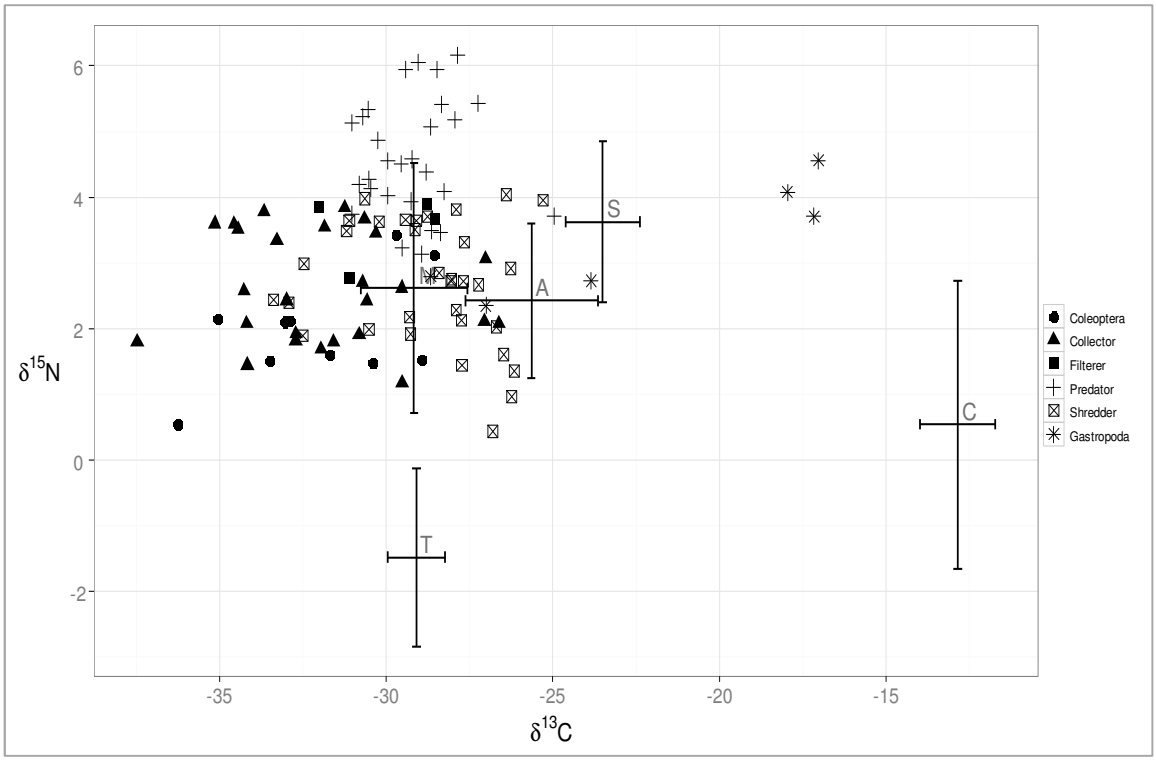


Fig. 6.1.2 Distribution of invertebrate feeding groups from the regulated Tooms River (upper panel) and the unregulated Macquarie River (lower panel) against the δ^{13} C and δ^{15} N signatures of the combined food resource groups: algae (A), cyanobacteria (C), emergent macrophytes (M), terrestrial sources (T) and submerged macrophytes (S). Invertebrate groups are indicated by the symbols shown in the legend.

Table 6.1.3 Significance values for invertebrate functional feeding group $\delta^{13}C$ signatures between sites and rivers. n.a. indicates that the feeding group was not available for that site combination; **, $0.001 < p < 0.01$; ***, $p < 0.001$; n.s., non-significance at the 0.05 level.

Functional feeding group	Regulated vs. unregulated Mean $\delta^{13}C$	Regulated upstream vs. downstream Mean $\delta^{13}C$	Unregulated upstream vs. downstream Mean $\delta^{13}C$	Pairwise comparisons
Collector-gatherers	-25.79 vs. - 31.89 ***	-22.17 vs. -26.62 **	-32.16 vs. -31.56 n.s.	Tooms upstream different to both unregulated sites ($p < 0.0001$)
Filter feeders	-23.68 vs. -30.11 ***	-24.36 vs. -23.46 n.s.	n.a.	Macquarie downstream different to both regulated sites ($p < 0.03$)
Benthic predators	-22.29 vs. -29.35 ***	-20.6 vs. -23.21 ***	-29.412 vs. -29.296 n.s.	Macquarie sites non-significant. All other comparisons significant ($p < 0.004$)
Scraper-grazers				
Gastropoda	-13.63 vs. -21.94 n.s.	– 14.25 vs. -11.77 n.s.	-17.03 vs. -22.928 n.s.	Gastropoda non-significant
Coleoptera	-25.27 vs. -32.00 ***	n.a.	n.a.	Coleoptera single sites
Shredders	-23.70 vs. -28.74 **	-19.49 vs. -26.51 **	-28.7 vs. -28.79 n.s.	Tooms upstream different to all other sites ($p < 0.03$)

Table 6.1.4 Mean $\delta^{13}C$, $\delta^{15}N$ and carbon to nitrogen ratios of food source groups, ± 1 standard deviation, for each river

Food source	River	Algae	Cyanobacteria	Emergent macrophytes	Submerged macrophytes	Terrestrial
Mean $\delta^{13}C$	Tooms	-25.71 ± 2.13	-12.93 ± 1.11	-28.95 ± 0.90	-21.97 ± 2.44	-29.20 ± 1.08
	Macquarie	-25.45 ± 1.34	-12.53 ± 1.02	-29.24 ± 1.72	-23.53 ± 1.02	-29.07 ± 0.70
Mean $\delta^{15}N$	Tooms	2.22 ± 1.10	1.00 ± 1.94	2.09 ± 2.00	2.92 ± 1.81	-1.79 ± 1.34
	Macquarie	2.94 ± 1.06	-1.28 ± 2.01	2.81 ± 1.74	3.71 ± 0.74	-0.95 ± 1.96
C: N ratio	Tooms	12.57 ± 5.77	21.76 ± 4.46	25.95 ± 11.22	11.16 ± 2.44	70.03 ± 31.93
	Macquarie	15.19 ± 2.16	10.19 ± 5.24	19.00 ± 9.08	18.18 ± 6.46	67.20 ± 23.48

The differences between the regulated and unregulated rivers persisted when considering only those taxa that occurred in both rivers. The stable carbon values for consumers in the unregulated Macquarie were, on average, 6.8‰ lower (range: 2.1 to 11.3‰) than the same consumers present in the regulated Tooms (Table 6.1.5).

Table 6.1.5 Mean $\delta^{13}C$ (± 1 SD) values of macroinvertebrates common to the Macquarie and Tooms Rivers.

Family (Order or Class)	Species	Tooms $\delta^{13}C$ (‰)	Macquarie $\delta^{13}C$ (‰)
Psephenidae (Coleoptera)	*Sclerocyphon aquaticus* Lea	-25.72 ± 1.08	-32.72 ± 2.22
Simuliidae (Diptera)	*Austrosimuliium* sp. Tonnoir	-24.15 ± 0.21	-30.11 ± 1.48
Leptophlebiidae (Ephemeroptera)	*Atalophlebia albiterminata* Tillyard	-25.64 ± 0.92	-30.60 ± 2.03
	Koorrnonga sp. AV1 Campbell & Suter	-29.44 ± 1.08	-31.58 ± 1.28
Physidae (Gastropoda)	*Physidae* spp. Fitzinger	-15.86 ± 2.80	-26.51 ± 1.99
Gripopterygidae (Plecoptera)	*Leptoperla varia* Kimmins	-22.55 ± 2.29	-33.87 ± 1.94
Eusthenidae (Plecoptera)	*Eusthenia spectabilis* Gray	-22.88 ± 0.67	-28.26 ± 0.40
Ceinidae (Amphipoda)	*Austrochiltonia* sp. Hurley	-19.49 ± 2.39	-29.35 ± 1.91

Scrapers were the only feeding group to show a significant difference in $\delta^{13}C$ signatures between the two Macquarie sites ($t_{(20)} = 2.443$, $p = 0.023$). However, the more depleted values at the upstream site were driven by the absence of Psephenidae from the downstream site, and there were no differences between these sites when this taxon was excluded. Of the Tooms River sites, by contrast, all feeding groups

except gastropods were significantly more $\delta^{13}C$ depleted at the downstream site, although this site remained significantly more $\delta^{13}C$ enriched than the Macquarie sites.

Resource use differed significantly between the regulated and unregulated rivers. Tooms River invertebrates had a mixed diet, dominated by algae, cyanobacteria and submerged macrophytes. In contrast, emergent macrophytes dominated Macquarie River invertebrate diets, with cyanobacteria less important than any other food source.

The diets of collectors and shredders showed the greatest difference between rivers (Fig. 6.1.3). Submerged macrophytes were up to 60% of the diet of collectors from Tooms River, with terrestrial sources less important than all other sources. Submerged and emergent macrophytes each formed up to 50% of Macquarie collector diets. *Paratya australiensis*, found only in the Macquarie River, recorded a mean $\delta^{13}C$ of -29.23‰, which indicated a diet high in terrestrial sources and macrophytes.

Shredders in Tooms consumed a mixed diet, with cyanobacteria and submerged macrophytes slightly more important than other sources, but cyanobacteria were an insignificant proportion of collector and shredder diets in the Macquarie. Emergent macrophytes were 50 – 60% of Macquarie shredder diet, with algae the second most important food group. The shredder Nymphulinae, also restricted to the Macquarie River, had an enriched mean $\delta^{13}C$ of -22.19‰, which would suggest a submerged macrophyte diet.

Benthic predator isotope values closely reflected the values of collectors in Tooms River, with submerged macrophytes dominating the dietary signal. In the Macquarie, in contrast, predator and shredder carbon isotope values were similar, indicating that shredders were a major prey item for predators in this river.

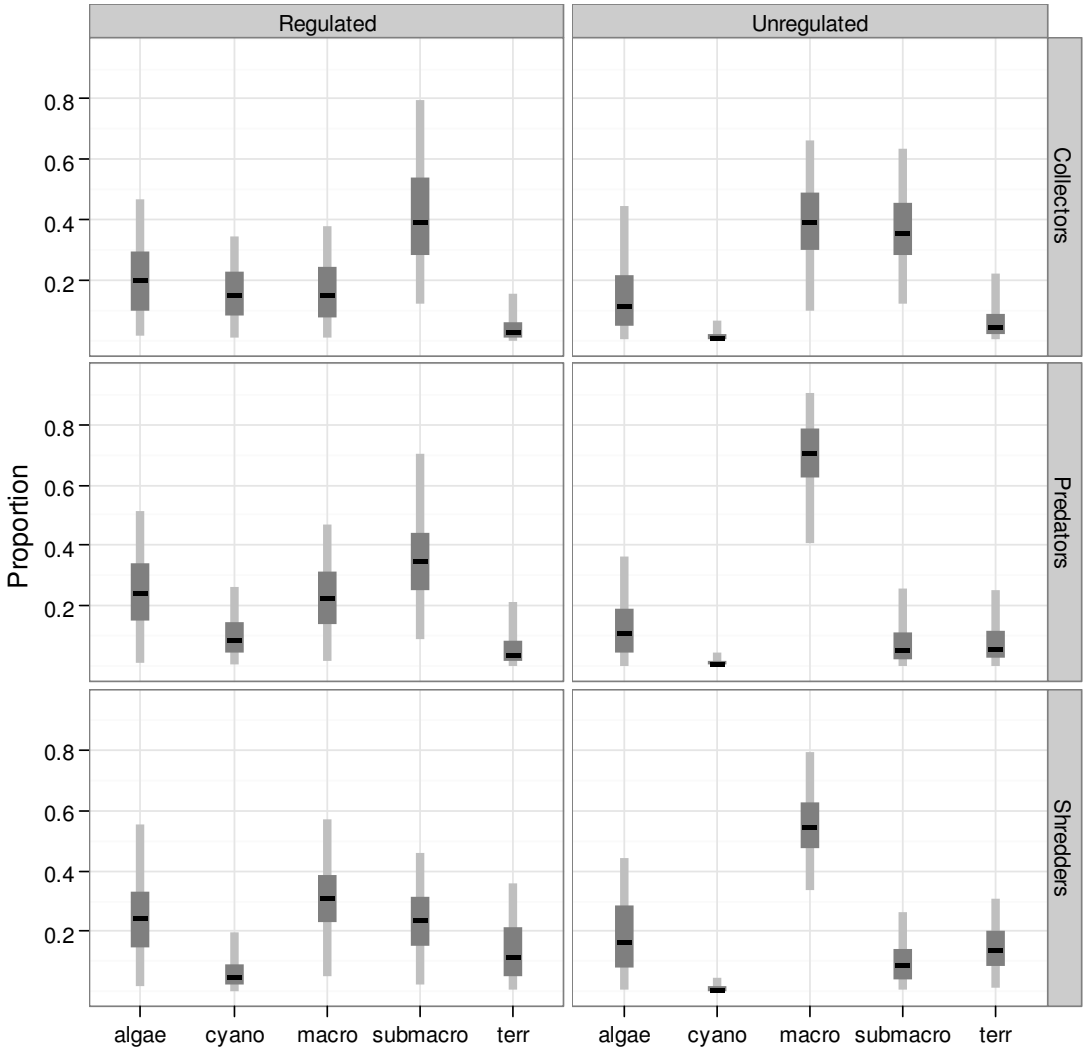


Fig. 6.1.3 Proportions of each food group in collector (upper panel), predator and shredder (lower panel) diets in the regulated Tooms River (left) and unregulated Macquarie River (right) , where the groups are left to right in each panel: algae, cyano = cyanobacteria, macro = emergent macrophytes, submacro = submerged macrophytes, terr= terrestrial sources. The boxes and whiskers indicate the 50% and 95% Bayesian confidence intervals, with the median values as a black horizontal bar.

A consistent pattern of food source assimilation was shown by filter feeders and scraper–grazers in each river (Fig. 6.1.4). Coleoptera were only collected from the downstream Tooms site and the upstream Macquarie site. In Tooms River they had a mixed diet, with no food group dominating the dietary proportions, whereas up to 60% of

Coleoptera diet in the Macquarie River was emergent macrophytes. However, *Sclerocyphon aquaticus* (Psephenidae) collected from pools choked with algae in the Macquarie River had a higher mean $\delta^{13}C$ value (-28.94‰) than the same species collected from macrophyte dominated pools (-33.49‰), demonstrating the influence of source availability on invertebrate diets. Overall, gastropod diet did not significantly differ between rivers, although there were differences in some species. Cyanobacteria were more important to Tooms gastropods, while terrestrial sources contributed more to gastropod diets than to coleopteran diets in both rivers (Fig. 6.1.4). Terrestrial sources were more important overall to Macquarie invertebrate diets than to Tooms invertebrate diets.

No sources formed more than 30% of Tooms filterer diets. In contrast, macrophytes were most important in Macquarie filterer diets, with equal proportions of algae, submerged macrophytes and terrestrial sources (Fig. 6.1.4), although filterers were only found at the downstream site. Although the difference was insignificant, cyanobacteria were a greater proportion of filterer diets than any other feeding group from the Macquarie.

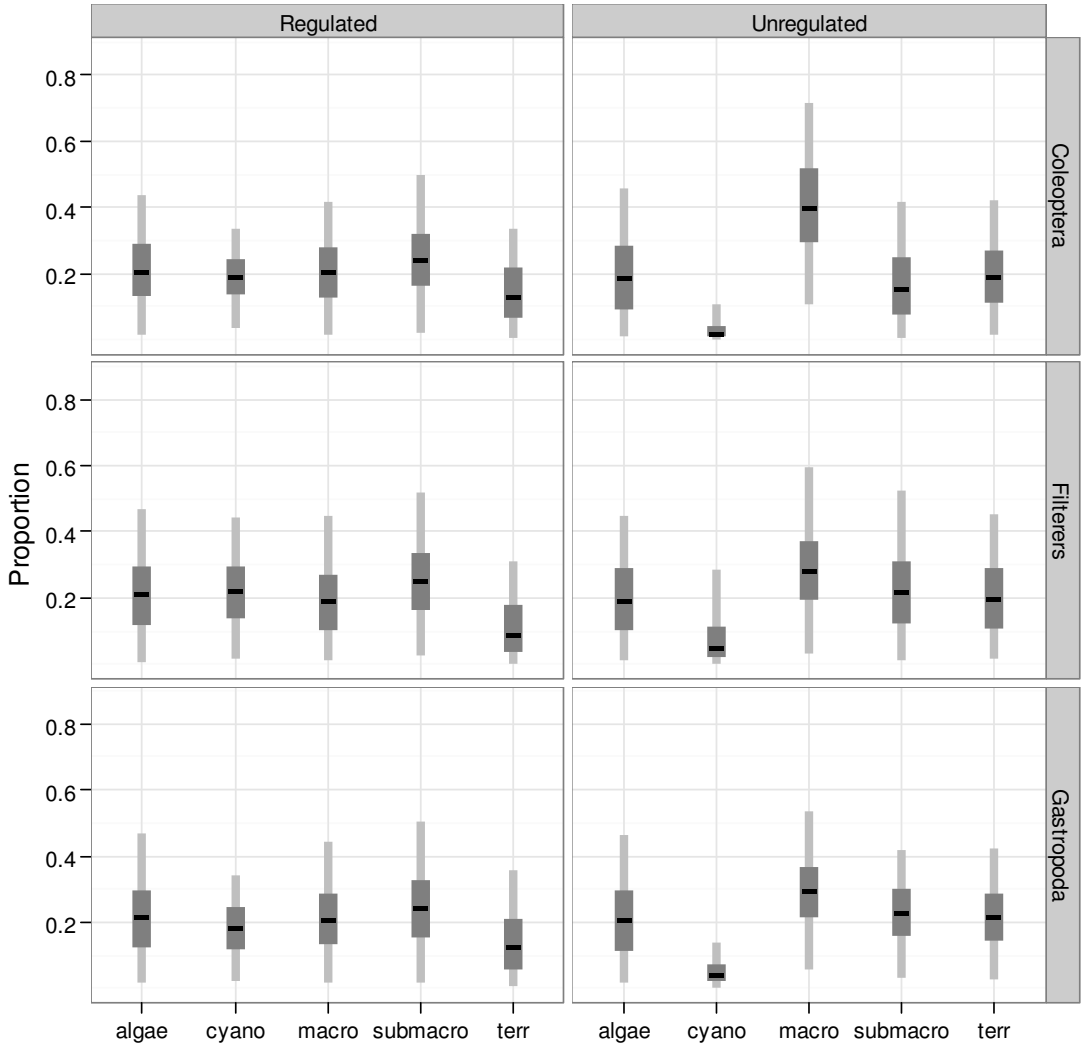


Fig. 6.1.4 Proportions of each food group in Coleoptera (upper panel), filterer and Gastropoda (lower panel) diets in the regulated Tooms River (left) and unregulated Macquarie River (right) , where the groups are left to right in each panel: algae, cyano = cyanobacteria, macro = emergent macrophytes, submacro = submerged macrophytes, terr= terrestrial sources. The boxes and whiskers indicate the 50% and 95% Bayesian confidence intervals, with the median values as a black horizontal bar.

Invertebrate $\delta^{15}N$ values did not differ significantly (ANOVA, all $p > 0.1$) between sites or rivers, except where highly $\delta^{15}N$ enriched values were shown by *P. australiensis* (4.8‰) and Nymphulinae (7.18‰), at the Macquarie sites. These species were absent from the Tooms River sites. Nymphulinae had the highest $\delta^{15}N$ of the Macquarie invertebrates, similar to the scavenging flatworm, *Cura* sp. (7.99‰), the most enriched

predator in Tooms River. Predators in the Macquarie were more $\delta^{15}N$ enriched than the same taxa in Tooms, although there were insufficient Tooms River samples for statistical testing.

Invertebrate isotope signatures did not differ significantly between seasons in Tooms River (Table 6.1.6). In the unregulated Macquarie River, the only seasonal effect was for predators, which were significantly more $\delta^{13}C$ enriched (ANOVA, $F_{(5, 24)} = 4.619$, $p = 0.0043$) in spring 2007 and summer 2007- 08 than in summer 2006- 07 and 2008- 09 (all $p < 0.03$). Gastropoda diets were more enriched in $\delta^{13}C$ and $\delta^{15}N$ in spring 2007 than in other seasons, suggesting the influence of macrophytes in their diet, but there were insufficient samples for statistical significance.

Table 6.1.6 Mean δ^{13} C and δ^{15} N signatures ± 1 SD where there were multiple samples, of the main feeding groups of macroinvertebrates in each river in each season. n.a = not available in that collection round

Season	Collectors		Gastropoda		Shredders		Predators	
	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N
Summer 2006- 07								
Macquarie R	-30.17 ± 1.02	2.90 ± 1.50	n.a	n.a	-29.45 ± 1.66	2.82 ± 0.60	-29.43 ± 0.98	4.83 ± 0.85
Tooms R	-23.84 ± 0.15	1.63 ± 0.88	-12.94 ± 1.16	3.76 ± 0.005	-25.55	1.55	-20.61 ± 2.15	4.41 ± 0.17
Autumn 2007								
Macquarie R	-31.95 ± 1.59	4.14 ± 0.48	-20.50 ± 3.34	3.22 ± 0.45	-28.76 ± 1.52	3.48 ± 0.74	-29.26 ± 1.14	4.76 ± 1.09
Tooms R	n.a	n.a	n.a	n.a	n.a	n.a	n.a	n.a
Winter 2007								
Macquarie R	-32.79 ± 3.33	3.86 ± 1.46	-28.66	2.8	-29.34 ± 3.01	2.77 ± 0.58	-29.30 ± 0.26	5.28 ± 0.78
Tooms R	-23.31 ± 2.16	3.18 ± 1.34	-14.18	4.27	-22.89 ± 4.10	2.22 ± 0.59	-22.53 ± 1.14	5.46 ± 1.24
Spring 2007								
Macquarie R	-31.15 ± 1.30	2.87 ± 1.16	-17.50 ± 0.46	4.32 ± 0.24	-27.84 ± 1.65	3.07 ± 0.89	-26.82 ± 1.38	4.41 ± 0.73
Tooms R	-27.27 ± 1.86	3.05 ± 1.20	-14.46	4.9	n.a	n.a	-21.78 ± 2.09	5.71 ± 1.34
Summer 2007- 08								
Macquarie R	-27.86 ± 2.98	3.43 ± 1.04	n.a.	n.a.	-27.72	1.44	-26.60 ± 1.65	3.90 ± 0.18
Tooms R	-27.05 ± 0.97	2.36 ± 0.98	n.a	n.a	-21.88	2.07	-23.70 ± 1.36	4.62 ± 0.33
Summer 2008- 09								
Macquarie R	-31.30 ± 2.70	2.86 ± 0.89	-27.01	2.35	-28.03 ± 2.53	2.29 ± 1.84	-29.70 ± 0.91	4.23 ± 0.60
Tooms R	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

The regulated Tooms River had significantly higher total nitrogen, total phosphorus and total organic carbon concentrations than the Macquarie River sites (Table 6.1.7) but there were no significant differences between sites on each river.

Table 6.1.7 Significant differences between the regulated Tooms River and unregulated Macquarie River for total dissolved nitrogen and phosphorus and total organic carbon concentrations in water samples (milligrams per litre), showing the mean values ($\bar{x}$) ± 1 standard deviation.

Variable (mg.L^{-1})	Tooms $\bar{x}$ (n = 26)	Macquarie $\bar{x}$ (n = 22)	F	p
Nitrogen	0.47 ± 0.130	0.28 ± 0.131	9.958	0.0049
Phosphorus	0.017 ± 0.005	0.007 ± 0.002	24.967	< 0.0001
Carbon	17.13 ± 5.390	6.75 ± 2.195	24.629	< 0.0001

6.1.5 Discussion

River regulation plays a central role in the availability of food resources in Tooms River, and the nutrient concentrations in the water column, with flow-on effects to macroinvertebrate diets. In contrast to the Macquarie River, where the abundance of allochthonous and autochthonous resources varied seasonally, Tooms River resources were dominated by cyanobacteria and biofilms throughout the year (Chapter 4). The high biomass of leafy detritus in Tooms River did not form an important part of invertebrate diet, but may have provided a substrate and contributed dissolved organic carbon for algal and cyanobacterial growth. Allochthonous resources made up a greater proportion of Macquarie River invertebrate diets than of Tooms River diets, but were less dominant than expected for either river given the conspicuous abundance of this resource.

In direct contrast to other studies (e.g. Chester and Norris 2006; Chessman *et al.* 2009a), the few invertebrate species common to both rivers were consistently more $\delta^{13}C$ depleted at the unregulated sites, although the $\delta^{13}C$ signatures of the source materials did not differ between rivers. Tooms River is unlike these regulated streams in that its biofilms are not dominated by filamentous algae, which have depleted $\delta^{13}C$ signatures (Feminella *et al.* 1989). Although reduced turbidity below many dams promotes filamentous algal growth (e.g. Angradi 1994), filamentous algae in Tooms River are likely to be suppressed by the high turbidity and canopy shading.

Nevertheless, thick biofilms have developed with the reduction in spate frequency. The thicker boundary layer that develops in slow-moving water increases diffusion of the heavier ^{13}C isotope during photosynthesis (Hill and Middleton 2006), so that plants in slow-moving water tend to be more enriched in $\delta^{13}C$ than those in fast-moving water (Osmond *et al.* 1981; Keeley and Sandquist 1992; France and Cattaneo 1998). Carbon δ^{13} enrichment can also result from nutrient and light limitation of photosynthesis in thick biofilms (Hill and Middleton 2006).

More depleted $\delta^{13}C$ signatures are often found in seasonally warm pools, where cycling between daytime photosynthesis and nightly respiration by concentrated algal biomass results in ^{12}C enrichment (Keeley and Sandquist 1992). This is likely to have contributed to the depleted invertebrate $\delta^{13}C$ signatures at the unregulated sites, where invertebrates were mainly collected from remnant pools (Keeley and Sandquist 1992; France 1995; Keeley 1999).

The clear differentiation between emergent and submerged macrophytes as major food sources in each river was unexpected. The high turbidity and shade from overhanging riparian vegetation in Tooms River would be expected to suppress macrophytes and algal growth. Whereas several macrophyte species occurred in the Macquarie River,

macrophytes in Tooms River were restricted to *Potamogeton tricarinatus* F.Muell & A.Benn. Ex. A. Benn (1892) (Potamogetonaceae) in limited areas where the canopy was more open, with *Triglochin procerum* R. Br. (Juncaginaceae) in the lake littoral. It is likely that much of the macrophyte component of Tooms invertebrate diets came from decomposing *Triglochin* from the lake.

Cyanobacteria signatures separated sufficiently from other sources to indicate assimilation by most feeding groups in Tooms River. However, Estep and Vigg (1985) considered cyanobacteria inedible and Bunn and Boon (1993) thought them unimportant in wetland food webs. In contrast, Piola *et al.* (2008) found that cyanobacteria were important to *Paratya australiensis* in the Myall Lakes. Cyanobacteria were also prominent in gut contents in Murray River *P. australiensis* (Burns and Walker 2000a). *Paratya australiensis* was only found in the Macquarie River, but showed no affinity for cyanobacteria, which were rare in this river. The depleted $\delta^{13}C$ signature for *P. australiensis* indicated a reliance on either terrestrial detritus or macrophytes, which agrees with results for this species in an Australian wetland (Bunn and Boon 1993). Yam and Dudgeon (2005) suggested that Atyidae species may also ingest other macroinvertebrates, at least as scavengers, which is supported by the high mean $\delta^{15}N$ value for *P. australiensis* in the current study.

Bunn and Boon (1993) found that Crambidae larvae and leptocerid caddis flies had similar $\delta^{13}C$, but we found that Nymphulinae were significantly more $\delta^{13}C$ enriched than Leptoceridae. Surprisingly, Nymphulinae had the highest $\delta^{15}N$ signature of the Macquarie invertebrates, similar to the most enriched species in Tooms River. As Nymphulinae were found in cases made of and attached to *Myriophyllum*, it is unlikely that they were feeding on other invertebrates to the extent that they were the top predator. Examination of gut contents indicated a submerged macrophyte and

algal based diet, which agrees with the $\delta^{13}C$ value for this species. However, Vander Zanden and Rasmussen (2001) have demonstrated the high variability in detritivore $\delta^{15}N$ signatures, which they attributed to variable assimilation efficiencies and differential fractionation of highly variable food sources. Macquarie River predators were more $\delta^{15}N$ enriched than the same species in Tooms River, which may indicate a higher number of trophic levels in the Macquarie River.

The importance of autochthonous resources to invertebrate diets in both rivers reinforces the results of studies from tropical (Bunn *et al.* 1999; March and Pringle 2003; Brito *et al.* 2006) and sub-tropical (Bunn and Boon 1993; Hadwen *et al.* 2010a) streams and wetlands (Bunn *et al.* 1999; Bunn *et al.* 2003). In contrast, Reid *et al.* (2008) showed that allochthonous sources formed the major proportion of invertebrate diets in 3rd- and 4th–order central Victorian lowland streams, although agricultural development adjacent to the rivers may have influenced their results. Invertebrates from the intermittent Macquarie River did not consume substantial amounts of terrestrial resources. However, the prevalence of macrophytes in invertebrate diets in the Macquarie River could also be a response to seasonal intermittency. The increased water temperature in contracting pools may be a cue for invertebrates to maximize intake while high nutrient resources are available, as macrophytes had significantly higher nitrogen to carbon ratios than the terrestrial sources.

The contention of Bunn and Boon (1993) that the availability of allochthonous resources will be less important to aquatic food webs in regulated rivers than the distribution and abundance of algae, has been confirmed by this study. The regulated Tooms River is drawn from the naturally turbid Tooms Lake (Croome and Tyler 1972). The riparian vegetation contributes abundant leafy detritus, but shade and turbidity are likely to limit macrophyte growth. However, the stable flow regime encourages the growth of biofilms and cyanobacteria, which provide a

reliable and more palatable food source for invertebrates and drive the food web in Tooms River. While there was some recovery from impoundment at the downstream Tooms site, invertebrate diets at this site were still dominated by algae and cyanobacteria. In contrast, macrophytes dominated invertebrate diet in the unregulated Macquarie River, where turbidity is generally low. Although several authors have suggested macrophytes are not consumed by invertebrates (e.g.Bunn and Boon 1993; Boon and Bunn 1994), this result was verified with feeding preference trials, which showed that the macrophyte *Triglochin procerum* was preferred over terrestrial leaves (Watson and Barmuta 2011).

Both rivers are of similar size, have the same geology, climate and riparian plant communities, but the stable flow regime has modified the riparian vegetation structure at Tooms River, so that it is no longer like the Macquarie River. The marked shift in the assimilation of food resources was consistent across the multiple seasons of this study, with only predators from the Macquarie River showing a significant seasonal variation. Although this study covered two years of record drought, flows were reduced in both rivers, so the effects on stable isotope values are more likely to be due to regulation of the flow regime than to the drought, although the seasonal influence on predator diets was a direct effect of the changed community composition in response to the drought (Chapter 5).

There is an assumption that small dams (less than 15 m) will not seriously affect ecosystem values (WCD 2000) and that regulated river ecosystems will eventually reach a new equilibrium after an extended but undefined period (Petts 1984). There is pressure to impound smaller rivers with increasing demand for water resources, as most large rivers have already been dammed. However, significant differences in invertebrate isotope signatures are detectable 170 years after river impoundment. This implies that the changes to the flow

regime that result from small dams may have permanent impacts on food webs in regulated rivers. The effects detected in this study are unlikely to be unique to Tooms River. We propose that there will be similar shifts in the resource base in other regulated rivers in Mediterranean climate zones where the flow regime promotes riparian closure, as irrigation dams mature.

6.2 Macroinvertebrate feeding preferences

Watson, A. and Barmuta, L.A. 2011. Feeding preference trials confirm unexpected stable isotope analysis results: freshwater macroinvertebrates do consume macrophytes. *Marine and Freshwater Research* **62**: 1248-1257.

6.2.1 Abstract

The loss of connectivity in intermittent streams can limit aquatic invertebrate access to food resources, with different resources available in individual pools. Although leaf litter was abundant in the Macquarie River in Tasmania, stable carbon and nitrogen isotope analyses suggested that aquatic macrophytes were more prevalent in shredding macroinvertebrate diets. We tested this result with two multi-choice trials, which examined the feeding preferences of *Atalophlebia albiterminata* (Ephemeroptera) and the case-building trichopterans *Lectrides varians, Notalina bifaria, Triplectides similis* and *Triplectides ciuskus ciuskus*. We firstly tested preferences for the dominant benthic leaf species (*Acacia mucronata*, *Eucalyptus amygdalina*, *E. barberi*, *E. obliqua* and *E. viminalis*). We hypothesised that macroinvertebrates would preferentially select leaves with lower chemical concentrations, but there were no strong preferences for conditioned leaves by any invertebrate, although the leaves varied in toughness, tannin, nitrogen and allelochemical content. Secondly, we examined the preferences for *E. amygdalina* and *E. barberi* leaves or the fresh macrophytes *Triglochin procerum, Myriophyllum salsugineum* and *Potamogeton tricarinatus*. Macrophytes were preferred over leaves by all invertebrates, with *T. procerum* significantly preferred to the other macrophytes. This suggests that macrophytes may be undervalued in riverine food webs, and should be included in analyses of food webs using stable isotopes.

6.2.2 Introduction

The availability and nutritional value of allochthonous and autochthonous resources have been associated with aquatic invertebrate abundance and community composition (e.g. Cummins *et al.* 1989; Thorp and Delong 1994) and growth rates (Graça 2001; Lieske and Zwick 2007). In the drier regions of temperate Australia, many rivers are seasonally or supra-seasonally intermittent, with residual pools containing substantial biomass of leafy terrestrial detritus and living vascular macrophytes.

Insect food preferences are a compromise between optimising nutritional needs and avoiding allelochemicals in living and senescent leaves (Behmer 2009). The preferences of shredding invertebrates (sensu Cummins 1973) can be affected by the nutritional values of the leaves, and their residual chemical and physical defences (Bryant *et al.* 1983; Irons 1988). In Australian rivers, eucalypt and acacia leaves present challenges for invertebrate consumption, including toughness (Sanson *et al.* 2001), the presence of secondary metabolites (Cork 1996; Cooper 2001), low nitrogen concentrations, and high concentrations of tannins and other phenolics (Lodge 1991). Invertebrate feeding preferences can be strongly influenced by plant phenolic content (Lodge 1991), although many tannins are generally regarded as water-soluble (Bettelheim and March 1984). Eucalypts also contain other, usually water-soluble, secondary compounds that can deter invertebrate herbivory, most notably formylated-phloroglucinols (FPGs) (Cooper 2001), which are correlated with the toxic monoterpene 1,8-cineole (Koschier and Sedy 2001). In addition, eucalypt oils and waxes contain insoluble flavonoids, *n*-alkanes and tripterpenes (Li 1993), all of which may deter insect feeding (Bernays and Chapman 1994; Cooper 2001).

During a prolonged drought (2006 -2008), the remnant pools in the upper Macquarie River in eastern Tasmania varied in the availability of algae, vascular aquatic macrophytes (hereafter “macrophytes”) and

allochthonous detritus. Several studies (e.g.Hamilton *et al.* 1992; Bunn and Boon 1993) have discounted macrophytes as an aquatic invertebrate food source. However, Jacobsen and Sand-Jensen (1992) noted that the perception that macrophytes are rarely consumed by invertebrates has been largely based on field observations, where herbivory has been masked by the rapid growth of macrophytes. Nevertheless, living vascular macrophytes are still excluded from food web studies, with Hadwen *et al.* (2010b) providing a recent example.

As part of a larger study of resource availability, we employed stable carbon and nitrogen isotope analyses to examine macroinvertebrate use of resources. Unexpectedly, these analyses indicated that macrophytes dominated shredder diets, which prompted this investigation of how the remaining, dominant invertebrate consumers selected between the available food resources.

In contrast to terrestrial leaves, vascular macrophytes (here defined as 'rooted aquatic plants') are unlikely to have water-soluble leaf chemicals (Bärlocher 1997), and most are softer (Suren 1989) and richer in nitrogen (Newman 1991) than terrestrial plant leaves. Jacobsen and Sand-Jensen (1992, 1994) have shown that macrophytes can be an important food source for shredders, at least in some seasons (Reid *et al.* 2008). St. Clair (1994) observed larval Leptoceridae (Trichoptera) feeding on vascular macrophytes in a laboratory study, but suggested that food preference was heavily influenced by the availability of resources at the collection site. However, access to preferred food resources may be restricted in rivers that seasonally dry to pools (Reid *et al.* 2008) or during drought (Lake 2003).

Therefore, to confirm and extend our insights from stable isotope analyses, we conducted two multi-choice feeding preference trials for the terrestrial plant species that contributed most of the benthic leaf litter, and the most abundant macrophyte species at the study sites.

Based on the known chemical compositions of the oils and waxes of Tasmanian eucalypts (Li 1993), we hypothesised that the invertebrates would prefer the leaves with the lowest percentages of the compounds recognised as suppressing invertebrate consumption in eucalypts (Li 1993). We further hypothesised that the softer leaves and higher nutritional value of vascular macrophytes would make them more attractive than terrestrial leaves to herbivores.

6.2.3 Methods

Macroinvertebrates and potential food sources were collected from each of two sites on the upper Macquarie River in eastern Tasmania (Table 6.2.1). The Macquarie River system shares many of the characteristics of southeast Australian rivers, including high seasonal variability and intermittent flow (Lake *et al.* 1985). The region has a mean annual rainfall of about 500 mm, but had less than 380 mm per year during the study period, the lowest on record (Bureau of Meteorology 2010). Both sites were in natural dry eucalypt woodland, with a distinct riparian band dominated by *Acacia mucronata* and *Leptospermum* spp., and with mature eucalypt species set back from the river edge.

Table 6.2.1 Characteristics of the study sites on the Macquarie River

Site variables	Site A	Site B
Latitude	42°09'2.97"S	42°09'51.03"S
Longitude	147°49'59.04"E	147°42'43.73"E
Catchment area (km^2)	85. 9	169.3
Orientation of channel	ENE-WSW	E-W
Discharge ($m^2\ s^{-1}$)	0 - 130	0 – 131.3
Mean annual runoff	23669.40	41499.71
Altitude (m)	408	290
Mean bankful width (m)	8.9	5.1

6.2.3.1 Stable isotope analyses

Live invertebrates were collected from remnant pools in the Macquarie River, by sweeping with a pond net and by hand-picking from stones and detritus. Samples were collected quarterly between December 2006 and January 2008. Invertebrates were transported on ice to the laboratory and maintained in filtered river water for at least 24 h to void gut contents, with individual Trichoptera placed in separate containers to prevent case consumption. After freezing, invertebrates were cleaned of attached algae under a dissecting microscope, dried (48 h, 40^{o} C), then ground to a fine powder with a glass mortar and pestle. Conditioned leaves and leaves of vascular macrophytes were collected from the river bed and banks. Whole rocks were transported on ice, in sealed bags of stream water, to the laboratory. Biofilms and *Nostoc* colonies were scraped from rocks with a scalpel blade and foreign material removed under a dissecting microscope. All plant and algal samples were rinsed with distilled water before drying (48 h, 40^{o} C) and grinding with a mortar and pestle.

Stable isotope ratios and percentage carbon and nitrogen were measured on a 20/20 continuous flow isotope analyser (Europa Scientific, Franklin, Ohio, USA) at the Stable Isotope Unit at Waikato University, New Zealand. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as parts per thousand ($^{0}/_{00}$) difference between the samples and conventional standards.

Macroinvertebrates were assigned to functional feeding groups (sensu Cummins 1973) before statistical analyses, according to published Australian references (Chessman 1986; Growns and Davis 1994; Gooderham and Tsyrlin 2002), and augmented by local observations where necessary.

The SIAR (Stable isotope Analysis in R: Parnell and Jackson 2008) package (version 4) under R 2.11.2 (R Development Core Team 2010)

was used to assess the proportional contribution of the different food sources to each feeding group. Unlike the IsoSource mixing model (Phillips and Gregg 2003), SIAR incorporates variation in the carbon and nitrogen values of food sources, generating density plots of credible intervals for the estimated parameter (Parnell and Jackson 2008; Parnell *et al.* 2010). This procedure has been used in other recent stable isotopes studies of freshwater food webs (e.g. Giling *et al.* 2009). Credible intervals indicate posterior probability estimates (Edwards *et al.* 1963) and can be interpreted as Bayesian confidence intervals (Lee 1997). Carbon and nitrogen concentrations were incorporated in the model to down-weight the effect of high nitrogen values in some sources (Phillips and Koch 2002). We did not correct for carbon or nitrogen trophic fractionation in the model, because the trophic positions of the invertebrates in this study were unknown and introducing a fixed fractionation value could lead to erroneous results (McCutchan *et al.* 2003).

Food sources with overlapping signatures were grouped for analysis (Phillips *et al.* 2005) as shown in Table 6.2.2. Because analysis of variance showed that there was no significant difference in carbon isotope values of the food source groups between the two sites (all $p > 0.2$), the values were combined for all subsequent analyses.

Table 6.2.2. Food source groupings for stable isotope mixing model analyses, with mean δ13 C and δ15 N values for each group ± 1 standard deviation. The number of samples (n) tested in each group is given in parentheses.

Group	Description	Mean δ^{13} C	Mean δ^{15} N
Algae	Benthic diatoms, biofilms, floating algal mats (n = 8)	-25.99 ± 1.36	2.67 ± 1.37
Cyanobacteria	Cyanobacteria, primarily *Nostoc* colonies (n = 8)	-13.06 ± 0.37	0.63 ± 1.95
Emergent macrophytes	Emergent aquatic plants, assimilating atmospheric CO_2 (n = 12)	-29.11 ± 1.61	3.08 ± 1.58
Submerged macrophytes	Submerged aquatic plants, assimilating CO_2 or HCO_3^- (n = 10)	-23.65 ± 0.98	3.39 ± 0.95
Terrestrial	Terrestrial C_3 plants (n = 51)	-29.06 ± 0.82	-1.52 ± 1.31

6.2.3.2 Feeding preference trials

Two separate feeding preference trials were conducted to examine the stable isotope results. We collected taxa which were abundant in the remnant pools in the Macquarie River in February 2009 and considered likely to be shredders, consuming living or decomposing vascular plant material (Cummins 1973). These were the four Leptoceridae (Trichoptera) species *Triplectides ciuskus ciuskus*, *Triplectides similis, Lectrides varians* and *Notalina bifaria.* We also collected *Atalophlebia albiterminata* (Ephemeroptera: Leptophlebiidae), which we observed browsing on leaf material. Other Tasmanian Leptophlebiidae have been shown to shred leafy detritus (Yeates and Barmuta 1999) and Cheshire *et al.* (2005) classified *Atalophlebia* as shredders in tropical streams.

The first trial tested phyllodes (hereafter referred to as "leaves") of *Acacia mucronata* (Mimosaceae) and leaves of the four main riparian eucalypt species, *Eucalyptus amygdalina, E.barberi, E. obliqua*, and *E. viminalis* (Myrtaceae). All leaves were recently abscised, green or orange, and collected from trees adjacent to the study pools. The prevailing dry conditions meant that none had been exposed to any precipitation prior to collection. Prior to use in the trial, all leaves were conditioned in 500-µm mesh nylon bags for 2 weeks, to simulate natural benthic leaf condition. Because there was a high risk that the remnant pools in the Macquarie River would completely dry during conditioning, and potential for interference by vandals, leaves were conditioned in Lambert Creek, Sandy Bay (42° 54.6" S, 147° 19.8" E), which has similar climate, vegetation and geology to the Macquarie River. Both streams had circumneutral pH (Macquarie River (mean ± SE): 7.3 ± 0.4; Lambert Creek: 7.2 ± 0.3), with similar low conductivities (Macquarie River: 128 ± 42 µS cm^{-1} and Lambert Creek: 117 ± 52 µS cm^{-1}) and dissolved oxygen greater than 90% saturation in both water bodies during the period of study.

After conditioning, leaves were gently rinsed in distilled water and oven-dried to constant mass at 40° C. The disparity in leaf size and shape prevented a standard-sized fragment for the feeding trials. *Eucalyptus barberi, E. obliqua*, and *E. viminalis* leaves were cut with circular cork borers (10 mm, 12 mm and 15 mm respectively). This included the centre vein to reduce differences to the full width lengths cut for *E. amygdalina* (15 mm long x ~8 mm wide) and *A. mucronata* (40 mm long x 3-4 mm wide). Leaf pieces were individually weighed to 0.0001 g on a Mettler M3 UM3 balance and rehydrated for 2 days in stream water to reduce buoyancy.

Trials were established in individually aerated 150 x 100-mm PVC containers, filled to 30 mm with Macquarie River water, and maintained at a constant 15° C and 12 hour light:dark regime. A 30 - 45-mm diameter scrubbed river stone was placed in the centre of each container. Each container held one invertebrate, with all 5 leaf species, with 25 replicates for each invertebrate species. A further 25 containers were established as controls for natural decomposition, with all 5 leaf species but no invertebrates. At the conclusion of each trial, leaf pieces were dried and reweighed. Consumption was measured as the difference in mass between exposed leaf pieces and the controls. Animals were observed to move freely between the different leaf fragments during the 21- day trial, which provided observable feeding activity, but ensured that more than 50% mass of each leaf fragment remained, thus satisfying the assumptions of free choice in multi-preference feeding trials (Manly 1993, 1995).

There were few strong preferences between terrestrial leaves in this first trial, so our second trial tested preferences between terrestrial leaves and macrophytes. Each animal was offered a choice of the two eucalypt species which appeared to be best preferred in the first trial, *E. amygdalina* and *E. barberi,* and the fresh leaves of the macrophytes *Triglochin procerum* (Juncaginaceae), *Myriophyllum salsugineum*

(Haloragaceae), and *Potamogeton tricarinatus* (Potamogetonaceae), which were abundant in the pools. Submerged leaves were selected for all macrophytes, because the stable isotope analyses showed that submerged and emergent macrophytes had different $\delta^{13}C$ signatures (Table 6.2.2).

The second trial tested 20 replicates of each of four of the same invertebrate taxa plus 20 controls for autogenic changes. *Atalophlebia albiterminata, N. bifaria*, *T. ciuskus ciuskus* and *T. similis* were collected from the Macquarie River in March 2009. *Lectrides varians* was excluded from the second trial because the majority of animals had begun pupating as the remnant pools shrank, and we could not collect sufficient specimens.

Terrestrial leaves were processed as for the first trial. The macrophytes were washed in distilled water to remove attached epiphytes and cryptic invertebrates. Whole leaves were used for *P. tricarinatus*, with 40-mm *M. salsugineum* tips and 30-mm *T. procerum* lengths. Each section was blotted dry before initial and final mass were measured (0.0001 g). The second trial was discontinued after 8 days, with close to 50% of *T. procerum* fragments consumed in most containers.

Feeding preference was measured using the continuous version of the Chesson-Manly selection index (Chesson 1983; Manly 1995), β. This measures the degree of selection for food item i against the null hypothesis of no preference, following Yao's approximation of degrees of freedom test (Yao 1965; Manly 1993), with the formula:

$$\beta_i = \frac{\alpha_i}{\sum_{j-1}^{K} \alpha_j}$$

where a_i is the estimated mean of the natural logarithm of the proportion of food j remaining in the controls, minus the mean of the natural logarithm of the proportion of food j remaining in the container

of the given species. If the null hypothesis is true, then $\beta_i = 1/K$ ($K = 5$ choices in these trials) indicates equal consumption of all foods; $\beta_i > 1/K$ indicates preference for food type i and $\beta_i < 1/K$ indicates avoidance of food i. The significance of each β_i was assessed by computing Bonferroni-corrected 95% confidence intervals following Manly (1995) and inspecting the confidence interval to determine if it included the value $1/K$.

To explore whether feeding preferences were related to any chemical or physical attributes of the terrestrial leaves, Pearson correlation coefficients, r, were calculated between the $\underline{\beta}_i$ values for each invertebrate species and the physicochemical variables of the leaves, as follows, with correlations > |0.7| considered large (p-values in this context are meaningless, so inspecting the size of correlation coefficients is the more useful exploratory tool: Chatfield and Collins 1980). Carbon and nitrogen concentrations of the leaf and macrophyte species were obtained from the stable isotope analyses. The condensed tannins remaining in the conditioned terrestrial leaves were assayed with acid butanol (Hagerman 1995). Absorbances were measured with a Cary 1E UV–Visible spectrophotometer (Varian, Palo Alto, CA), with results expressed as equivalents of purified sorghum tannin in milligrams per gram of dry mass (mg g^{-1} DM equivalent ST). Li (1993) measured the chemical composition of Tasmanian eucalypt oils and waxes and secondary metabolites. The non-water soluble components likely to remain after conditioning in freshwater (Bettelheim and March 1984) are reported in Table 6.2.3. The only water-soluble compound included here is 1,8-cineole, because it is strongly correlated with the non-water soluble formylated-phloroglucinols (FPG) compounds, which are known to be strong deterrents to herbivores.

Because leaf toughness can influence invertebrate feeding preferences, toughness was measured for 10 replicates of each species of conditioned terrestrial leaves and fresh macrophyte leaves using a penetrometer,

with toughness calculated according to Nolen and Pearson (1993) as the force required to drive a vertical 1.55-mm diameter pin through each leaf.

Table 6.2.3. Physicochemical values and dominant insoluble components of leaves used in feeding preference trials. Component values are a percentage of the total oil or wax as extracted from adult leaves (Li 1993). The tannin assay values are for condensed tannins remaining in the leaves after conditioning. Soluble 1, 8 – cineole is included because it correlates with formylated-phloroglucinols (FPG) levels in some species.

Leaf species	Toughness (g)	Nitrogen (%)	C:N	Condensed tannins (mg g DM)	n-alkanes (%)	Flavonoids (%)	Triterpenoids (%)	a-phellandrene (%)	1,8-cineole (%)	p-cymene (%)
Eucalyptus amygdalina	848.1	0.8	61.2	34.4	6.7	13.4	31.4	16.0	49.6	7.5
Eucalyptus barberi	1100.3	0.9	54.3	28.5	61.6	5.2	1.9	0.2	72.4	0.7
Eucalyptus obliqua	1630.7	0.4	116.6	8.5	8.4	8.8	50.3	4.5	1.5	22.4
Eucalyptus viminalis	1127.3	1.0	52.1	20.5	9.2	10.9	4.3	4.2	14.3	4.1
Acacia mucronata	2902.9	1.2	46.6	36.2	-	-	-	-	-	-
Myriophyllum salsugineum	-	2.0	20.1	-	-	-	-	-	-	-
Potamogeton tricarinatus	86.2	2.6	17.0	-	-	-	-	-	-	-
Triglochin procerum	283.2	3.4	11.7	-	-	-	-	-	-	-

We used one - way analysis of variance (ANOVA) to examine whether there were significant differences in C: N ratios and toughness scores, which might help explain invertebrate feeding preferences. Two-tailed Student's *t*-test examined differences in total consumption between trials 1 and 2, to examine whether invertebrates varied their consumption rates with different resources. *Lectrides varians* larvae were excluded from this analysis because they were only tested in the first trial. Assumptions for all statistical tests were verified using standard graphical techniques, and no transformations were necessary (Quinn and Keough 2002). All computations were carried out in R version 2.9.2 (R Development Core Team 2009).

6.2.4 Results

6.2.4.1 Stable isotope analyses

The stable isotope mixing model clearly differentiated between the different food groups in shredder diets (Fig. 6.2.1). Emergent macrophytes were more important than submerged macrophytes, forming more than 60% of shredder diets. Algae formed up to 40% of diets, with minor proportions of terrestrial sources and cyanobacteria. The indication that emergent macrophytes formed a greater component of shredder diets than any other food source prompted feeding preference trials for terrestrial leaves and fresh macrophytes.

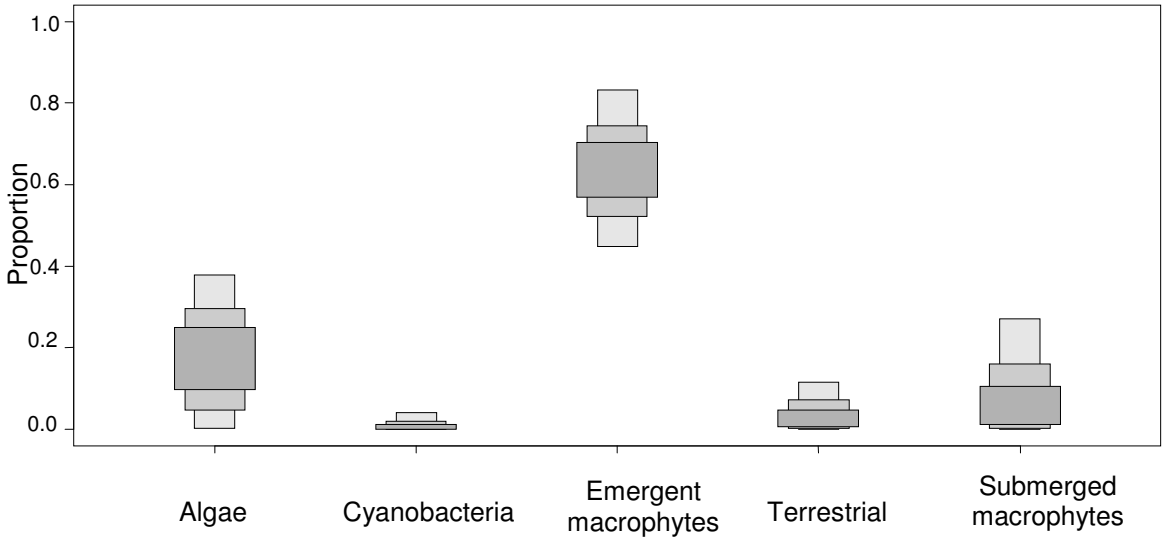


Fig. 6 2.1 Proportions of food source groups in diets of shredders from the Macquarie River sites, grouped by food source type. The density plots indicate the 50, 75 and 95% credible intervals as progressively lighter grey boxes.

6.2.4.2 Feeding preference trials

All animals except *T. similis* significantly avoided *E. obliqua* ($\beta_i < 0.2$) for food and case construction (Table 6.2.4). *Acacia mucronata* was significantly avoided by *L. varians,* but preferred by *Notalina bifaria*, although this was likely to be due to grazing on biofilms as there was no visible evidence of leaf consumption. *Lectrides varians* preferred *E. amygdalina* and *E. barberi,* while *T. ciuskus ciuskus* significantly preferred *E. viminalis*, with a marginally significant preference for *E. barberi.* In contrast, *T. similis* neither preferred nor avoided any plant species.

Table 6.2.4 Chesson-Manly index ($\hat{\beta}$) estimates for a multi-choice feeding trial between five terrestrial plant species for each of five macroinvertebrate species (n = 25). Significant preference ($p < 0.05$) for a particular plant species is indicated by $\hat{\beta} > 0.2$, where the 95% confidence interval (CI) does not overlap 0.2. $\hat{\beta} < 0.2$ indicates avoidance of a particular plant species. Significant preferences or avoidances are in bold.

	Eucalyptus amygdalina		*Eucalyptus barberi*		*Eucalyptus obliqua*		*Eucalyptus viminalis*		*Acacia mucronata*	
Invertebrate species	β	CI	β	CI	β	CI	β	CI	β	CI
Atalophlebia albiterminata	0.32	0.15-0.50	0.19	0.11-0.26	**0.00**	**0.00-0.16**	0.17	0.09-0.24	0.32	0.17-0.47
Notalina bifaria	0.25	0.10-0.41	0.18	0.05-0.31	**0.00**	**0.00-0.19**	0.12	0.03-0.22	**0.44**	**0.24-0.64**
Lectrides varians	**0.28**	**0.21-0.35**	**0.35**	**0.30-0.40**	**0.12**	**0.06-0.18**	0.23	0.19-0.26	**0.03**	**0.01-0.04**
Triplectides ciuskus ciuskus	0.17	0.06-0.28	0.26	0.13-0.39	**0.08**	**0.00-0.17**	**0.32**	**0.26-0.39**	0.16	0.07-0.25
Triplectides similis	0.24	0.00-0.83	0.76	0.00-1.00	0.00	0.00-0.87	0.00	0.00-0.57	0.00	0.00-0.59

There were few strong correlations between the invertebrate feeding preferences and the physicochemical variables of the leaves. *Acacia mucronata* retained more condensed tannins than the other terrestrial species, with the lowest tannin levels in *E. obliqua*. *Eucalyptus barberi* had high levels of *n*-alkanes and 1, 8-cineole, while *E. obliqua* had high triterpenoid and *p*-cymene levels. *Eucalyptus obliqua* was the toughest of the eucalypts, but slightly less than half as tough as *A. mucronata.* All the macrophytes were significantly softer than any of the terrestrial leaves (see Table 6.2.3).

Acacia mucronata had the highest nitrogen content of the terrestrial leaves, while *E. obliqua* contained significantly less nitrogen ($p = 0.001$) than the other species. The carbon: nitrogen ratio of the macrophyte species was significantly lower ($p = 0.016$) than for the terrestrial species.

Correlations between feeding preferences and physicochemical variables in the first trial differed between invertebrate species (Table 6.2.5). The strongest negative correlations were for chemicals which were abundant in the least preferred species, *E. obliqua* (triterpenoids and *p*-cymene), while strong positive correlations were with chemicals which were abundant in *E. amygdalina* or *E. barberi* (*n*-alkanes and 1, 8-cineole). Leaf toughness was only potentially important to *L. varians*. Both *A. albiterminata* and *N. bifaria* showed strong positive correlations with tannin concentrations, which were highest in *E. amygdalina* and *A. mucronata*. Only *T. similis* showed a strong correlation with the size of the leaf fragment.

Table 6.2.5 Pearson correlation coefficients between invertebrate terrestrial leaf preference (β) and physicochemical variables. All leaf chemicals except 1,8-cineole were insoluble in water. Although condensed tannins are considered water-soluble, the assay was for the condensed tannins remaining in the leaves after conditioning in flowing water. Large correlations ($r > |0.7|$) are in bold.

Variable	*Atalophlebia albiterminata*	*Lectrides varians*	*Notalina bifaria*	*Triplectides ciuskus ciuskus*	*Triplectides similis*
C: N ratio	**-0.82**	-0.21	**-0.74**	**-0.69**	-0.27
Toughness (g)	0.19	**-0.90**	0.58	-0.38	-0.46
Leaf fragment area	0.30	-0.25	0.16	0.24	**-0.71**
Tannins (mg g DM)	**0.98**	0.08	**0.91**	0.20	0.29
n-alkanes %	0.07	**0.72**	0.24	0.36	**0.93**
Flavonoids %	0.45	-0.25	0.30	-0.13	-0.64
a-phellandrene %	0.62	-0.02	0.51	-0.34	-0.30
Triterpenoids %	-0.40	**-0.74**	-0.47	**-0.96**	-0.52
1,8 - cineole %	0.68	**0.96**	**0.79**	0.32	**0.93**
p-cymene %	**-0.70**	**-0.90**	**-0.76**	**-0.87**	-0.62

Total consumption per day was significantly higher in the second trial, for all animals except *N. bifaria* (Fig. 6.2.2). *Atalophlebia*

albiterminata, T. ciuskus ciuskus and *T. similis* all consumed significantly more food when macrophytes were available than when only terrestrial leaves were available.

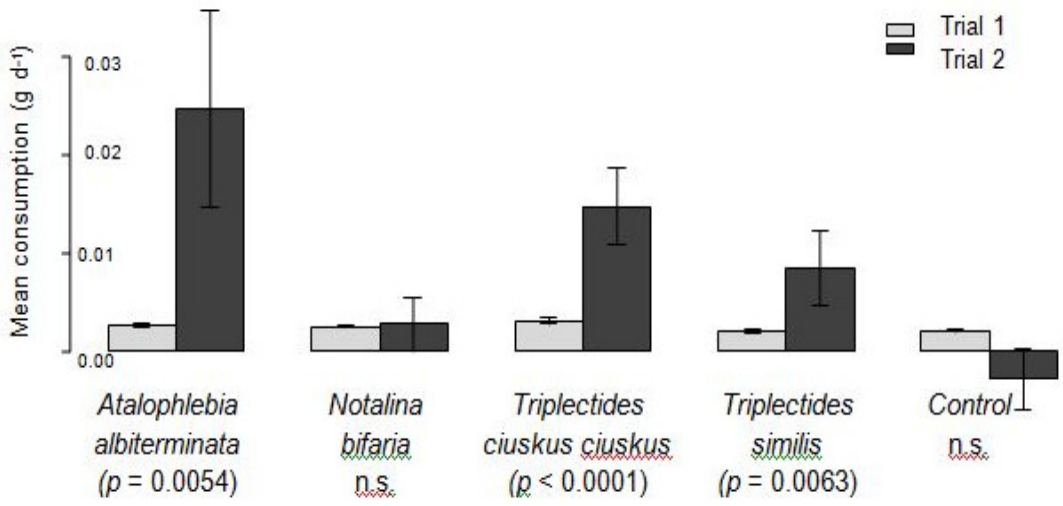


Fig. 6.2.2 Mean total consumption (g d^{-1}) for each invertebrate species between trial 1 and trial 2. Students t-test significance scores are shown below each species name.

There was almost no consumption of terrestrial leaves in the second feeding trial, with a highly significant preference for the emergent macrophyte *Triglochin procerum* by all animals except *N. bifaria. Myriophyllum salsugineum* tips continued to grow and several fragments developed roots, making visual detection of consumption difficult.

Atalophlebia albiterminata exclusively consumed *T. procerum* and significantly avoided all other plant species. While variation between individual animals was high, *Notalina bifaria* was the only species which showed any preference for a terrestrial leaf species. *Eucalyptus amygdalina* and *T. procerum* were marginally preferred, while *E. barberi* was avoided. Both *T. ciuskus ciuskus* and *T. similis* showed significant preferences for *T. procerum,* while avoiding all other plant species (Table 6.2.6).

Table 6.2.6 Chesson-Manly index ($\hat{\beta}$) estimates for a multi-choice feeding trial between two terrestrial plant species and three macrophytes for each of four macroinvertebrate species (n = 20). Significant preference ($p < 0.05$) for a particular plant species is indicated by $\hat{\beta} > 0.2$, where the 95% confidence interval (CI) does not overlap 0.2. $\hat{\beta} < 0.2$ indicates avoidance of a particular plant species. Significant preferences or avoidances are in bold.

	Eucalyptus amygdalina		*Eucalyptus barberi*		*Myriophyllum salsugineum*		*Potamogeton tricarinatus*		*Triglochin procerum*	
	β	CI	β	CI	β	CI	β	CI	β	CI
Atalophlebia albiterminata	**0.00**	**0.00-0.05**	**0.10**	**0.02-0.17**	**0.00**	**0.00-0.08**	**0.00**	**0.00-0.11**	**0.90**	**0.73-1.00**
Notalina bifaria	**0.00**	**0.00-0.17**	0.10	0.00-0.31	0.12	0.00-0.52	0.00	0.00-0.63	0.78	0.08-1.00
Triplectides ciuskus ciuskus	**0.03**	**0.00-0.10**	0.10	0.00-0.25	**0.06**	**0.00-0.15**	**0.00**	**0.00-0.16**	**0.80**	**0.56-1.00**
Triplectides similis	**0.00**	**0.00-0.05**	**0.01**	**0.00-0.07**	**0.07**	**0.00-0.18**	**0.00**	**0.00-0.18**	**0.92**	**0.68-1.00**

6.2.5 Discussion

The prevalence of aquatic macrophytes in the diets of invertebrates from the intermittent Macquarie River was unexpected. Reid *et al.* (2008) showed that allochthonous sources formed the major proportion of invertebrate diets in similarly sized central Victorian streams, but this was not supported in our study by either stable isotope analyses or feeding preference trials. Allochthonous material was a minor food source for most invertebrates, with few preferences for specific leaf types.

We expected that the invertebrates would prefer the terrestrial leaves with the lowest concentrations of insoluble chemicals. On this basis, *E. viminalis* should have been strongly preferred. However, there was little consistency in preferences between the invertebrates tested. Only *T. ciuskus ciuskus* significantly preferred *E. viminalis*. Both *L. varians* and *T. ciuskus ciuskus* preferred *E. barberi*, despite these leaves having moderately high concentrations of some allelochemicals. All the invertebrates tended to avoid *E. obliqua*. Although these leaves had the

lowest tannin and 1, 8-cineole concentrations, they had high triterpene and *p*-cymene concentrations, high C: N ratios, and were the toughest eucalypt species. The toughest leaf, *A. mucronata,* which also had the highest tannin concentration, was strongly avoided by only *L. varians.*

In contrast, the sequence of feeding preferences for macrophytes positively correlated with the C: N ratio of those species, with a clear preference for *Triglochin procerum* by most invertebrates. Russell-Hunter (1970) suggested that only plants with a C: N ratio of less than 17: 1 would supply sufficient nutrients to sustain animals. Of the plant species tested, only *T. procerum* and *P. tricarinatus* fitted this requirement. *Triglochin procerum* was more than 30% softer than the most preferred eucalypt species, but the toughest of the macrophytes. Deegan and Ganf (2008) and Reid *et al.* (2008) found that *Triglochin procera* was an important resource for some invertebrate species in summer. However, rapidly growing plants may have less chemical defences than slow-growing plants (Newman 1991). *Triglochin procerum* reached flowering stage less than 6 weeks after rehydration of the river bed, after 10 months with no surface water (A. Watson, pers. obs.). The submerged macrophytes *P. tricarinatus* and *M. salsugineum* were less prevalent in invertebrate diets than *T. procerum* and were actively avoided by most invertebrates in the feeding preference trials, although they had similarly low C: N ratios and were significantly softer than *Triglochin.* Friberg and Jacobsen (1994) showed that *Sericostoma personatum* (Trichoptera) and *Gammarus pulex* (Amphipoda) preferred conditioned *Alnus* leaves or filamentous algae to *Potamogeton perfoliatus*, despite this species having softer leaves and a higher nitrogen content. In contrast, Jacobsen and Sand-Jensen (1992) found that *Potamogeton* spp. leaves were seasonally preferred over other lake macrophyte species, although leaf morphology may have influenced their invertebrates' preferences. The avoidance of *Myriophyllum* species by some invertebrates has been attributed to the high phenol content of all the Haloragaceae (Choi *et al.* 2002). For example, *Acentria*

ephemerella (Lepidoptera: Crambidae) grew more slowly on a *Myriophyllum spicatum* diet than on a *Potamogeton perfoliatus* diet (Choi *et al.* 2002). Smolders (2000) showed that some *Potamogeton* species also had high phenol concentrations, although most species had lower tannin levels than *Myriophyllum*.

Interestingly, the second food choice for both *A. albiterminata* and *T. ciuskus ciuskus* was *E. barberi*, although it had a higher C: N ratio than the other two macrophytes and was significantly tougher. Jacobsen and Sand-Jensen (1992, 1994) proposed that shredding Trichoptera only ingested macrophytes when allochthonous material was unavailable. The preference for macrophytes over terrestrial plant species in the current study does not support these observations.

While oils and waxes have been cited as suppressing eucalypt leaf consumption (Fox and Macauley 1977; Ohmart and Edwards 1991) this was not supported by the current study. *Lectrides varians* significantly preferred *E. barberi*, despite this species having the highest concentration of *n*-alkanes of any Tasmanian eucalypt species and high 1, 8-cineole levels (Li 1993), which correlates with FPG concentrations (Foley and Lassak 2004). Although *n*-alkanes are considered to be indigestible by mammals (e.g. Bugalho *et al.* 2009), they are a component of insect exoskeletons and are known to be assimilated from dietary sources in some insects (Espelie *et al.* 1991; Hadley 1991).

Lectrides varians and *T. ciuskus ciuskus* showed a significant second preference for *E. viminalis,* although the insoluble flavonoids in *E. viminalis* leaves have been shown to inhibit insect feeding (Bernays and Chapman 1994; Harborne and Williams 2000). While *E. amygdalina* wax can be highly variable between locations, it can also contain high levels of flavonoids (Li 1993). Levin (1976) and Li (1993) both suggested that triterpene levels might attract herbivores. This may have been a

factor in the marginal preference for *E. amygdalina*, but conflicts with the avoidance of *E. obliqua,* the other species with high triterpene levels.

There were strong negative correlations between terrestrial leaf toughness and feeding preferences in the current study. The softest leaves, *E. barberi* and *E. amygdalina,* were preferred by all invertebrates except *T. ciuskus ciuskus*. The strongest preference was for macrophytes, which were significantly softer than terrestrial leaves. In contrast, eucalypt leaf toughness had no effect on *Antipodeus wellingtoni* (Amphipoda: Ceinidae) or *Caenota plicata* (Trichoptera: Calocidae) feeding preferences (Ratnarajah and Barmuta 2009), or *Anisocentropus kirramus* (Trichoptera: Calamatoceridae) larvae (Nolen and Pearson 1993).

St. Clair (1994) suggested that the availability of food resources was more important to invertebrate diets than feeding preferences. In her study, terrestrial leaf material was the main component of *Notalina bifaria* gut contents, but they ate *Myriophyllum* in feeding trials. She considered that *Notalina* spp. and *Triplectides* spp. were opportunistic feeders, as they consumed a mixture of terrestrial leaves and macrophytes when both resources were available. Despite visible shredding of *Myriophyllum* in one Macquarie River pool, *M. salsugineum* was not substantially consumed by the invertebrates tested in this study.

The factors influencing the results of the terrestrial leaf trial are inconclusive. The avoidance of *E. obliqua* is likely to be due to a combination of factors - high C: N ratio, toughness and allelochemical levels, although *E. obliqua* had the lowest condensed tannin content. While *Acacia mucronata* was generally avoided, it was the toughest species and had the highest tannin content. The reasons behind the preference for *E. barberi* by *L. varians* and *E. viminalis* by *T. ciuskus ciuskus*, and limited preference for *E. amygdalina* are less clear.

Eucalyptus barberi and *E. viminalis* were likely to have contained FPGs. Although *E. barberi* and *E. amygdalina* were the softest of the leaves tested, they had higher C: N ratios than all species except *E. obliqua,* the highest tannin content of all the tested eucalypts and also contained high levels of allelochemicals.

In contrast, the preference for the macrophyte, *T. procerum*, correlated with the lowest C: N ratio of any plant species tested, although it is unclear why the softer macrophyte species were avoided. Nevertheless, this result agrees with the stable isotope results, which indicated that these submerged macrophytes were less important to invertebrate diets. Interestingly, invertebrates consumed more resources per day in the second trial. This suggests that invertebrates are selecting *T. procerum* on the basis of nutritional content, and increasing consumption to take advantage of these nutrients, but that other untested factors influence their food choices when this resource is not available.

However, laboratory trials may not accurately reflect field conditions, where other factors can influence feeding preferences. For example, *Myriophyllum* tips continued to grow during the trial, with many fragments growing roots, which made detection of feeding activity difficult. *Myriophyllum* was included in the trial on the basis that it was heavily shredded in some remnant pools, but this was likely to be due to consumption by an untested invertebrate.

The results of this study suggest that macrophytes are a more important resource for invertebrates, at least in intermittent Australian streams, than has been reported in most other studies. A recent Australian study (Hadwen *et al.* 2010b) excluded macrophytes from the food sources in their stable isotope mixing model, on the basis that earlier studies had found macrophytes unimportant. In Sweden, Leberfinger *et al.* (2011) combined macrophytes and terrestrial leaves and grasses into a single category, CPOM, in their mixing model. In our

study, although macrophytes and terrestrial sources had similar δ^{13} C signatures, they could be clearly differentiated on the basis of their δ^{15} N signatures, as was also shown for a South American study (Hoeinghaus *et al.* 2007). The sclerophyllous eucalypt vegetation of temperate Australia is low in nitrogen (Fox and Macauley 1977), which may mean that distinguishing terrestrial leaves from macrophytes is simpler than in other regions. However, this may not be detected unless mixing models take both carbon and nitrogen values into account simultaneously, as occurs with the SIAR model (Parnell and Jackson 2008). The choice of the mixing model and the food sources included in the model can heavily influence the conclusions regarding resource use. As a consequence, this may have led to the underestimation of the importance of aquatic macrophytes to riverine food webs.

Chapter 7 General discussion

7.1 The impact of flow regulation on Tooms River

Although Walker (1979) identified research into the downstream effects of dams in Australia as essential, the focus has remained on large dams and deep-release reservoirs, largely because there is an expectation that small impoundments will not have a serious impact on stream ecosystems (e.g. WCD 2000; Nichols *et al.* 2006). Pohlon *et al.* (2007) even suggested that small dams may increase ecosystem health in some heavily impacted rivers.

The weight of evidence presented here however, suggests that the small dam which regulates Tooms River has had a permanent impact on the riparian vegetation, benthic resources, invertebrate community and aquatic food web. This vindicates McMahon and Finlayson's (2003) assertion that regulation of flow to produce an "anti-drought" regime will have profound effects on river ecology. Unlike the majority of regulated river studies, the effects of regulation of Tooms River can be isolated from land use practices and thermal effects from lake stratification. Therefore the observed effects are most likely a consequence of the reduction in flow variability and reversed seasonality of flow.

Table 1.1 listed the expected effects of flow regulation on ecosystem variables, based on examples from published literature. These are summarised in Table 7.1, which includes some additional hypotheses introduced in chapters 3 and 4, based on field observations. The final column shows whether these expectations were met in Tooms River.

Table 7.1 The predicted and observed outcomes of the effects of regulation of the flow regime on ecosystem variables, where √ = the prediction was met; X = the prediction was not met; ? = outcome unclear; na = not assessed. Citing references are listed in Table 1.1. Hypotheses introduced in chapters 3 and 4 are indicated with an asterisk *

Variable	Predicted outcome	Observed outcome
Flow regime	Reduced discharge, smaller floods, less frequent floods	√
Channel morphology	Contracted, incised channel	√
	Armoured bed	X
	Reduced channel complexity	?
	Reduced thalweg variability	?
	Fine sediment deposition	?
Riparian vegetation	Vegetation encroachment	√
	Reduced recruitment	√
	Reduced OM retention	X
	Altered species composition	√
	Reduced species richness	n.a.
	Higher litter fall *	√
	More variable litter fall *	X
	Higher soil organics *	X
	Higher decomposition *	X
Connectivity	Channel disconnected from floodplain	√
	Reduced interchange with hyporheic zone	n.a.
Water quality	Increased nutrients	√
	Altered dissolved oxygen concentrations	√
	Higher dissolved organic carbon *	√
Benthic leaf litter	Higher benthic leaf litter *	√
	Faster cellulose decomposition*	√
Algae and biofilms	Increased periphyton biomass	√
	Different biofilm species	√
	Heterotrophic biofilms *	X
	Reversed seasonality *	X
Macroinvertebrate communities	Reduced diversity	√
	More tolerant taxa	√
	Less sensitive taxa	?
	More rheophilic taxa	?

The majority of effects noted in other regulated river studies were also recorded in Tooms River, although geomorphological change has been limited because the dam is high in the headwaters, where the substrate is largely bedrock controlled, as noted by Petts (1979; 1993) and Benn and Erskine (1994). However, the channel has contracted and become incised, with the active channel much lower than the historic river terraces (Figs. 2.15, 2.16).

While some unexpected effects (e.g. more variable litter fall and reduced decomposition in the riparian zone) may have been a result of the drought, the delayed seasonality of litterfall was detected early in the study, and is likely to be a permanent effect of the more stable flow regime. Figure 7.1 models the positive and negative feedback effects on ecosystem variables, based on riparian and benthic litter dynamics under the current regulated flow regime, where peak litter fall coincides with summer high flows, and there are few floods or spates, and no cease-to-flow periods.

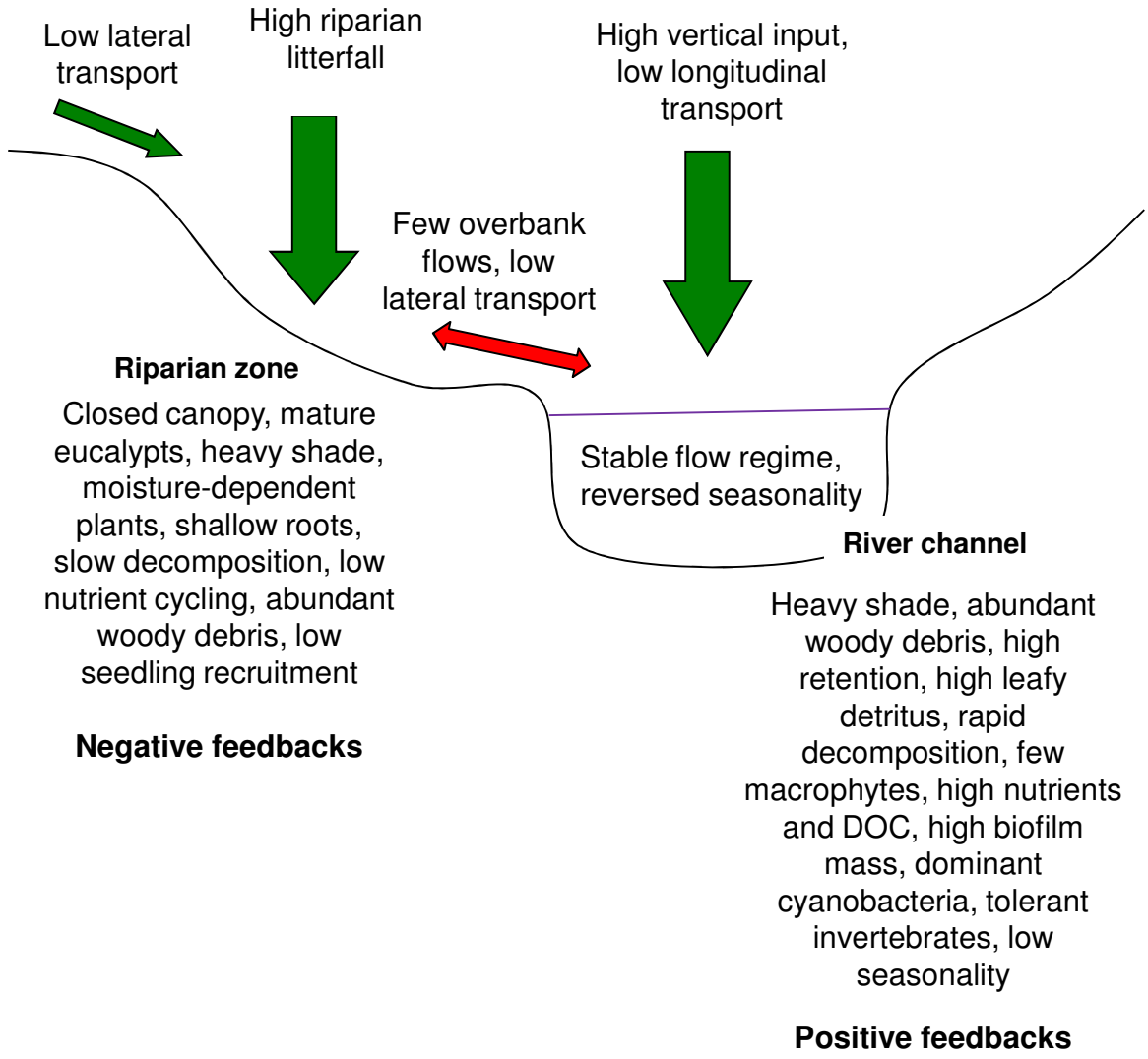


Fig. 7.1 Conceptual model of the dynamics of riparian and benthic resources in response to the stable flow regime of Tooms River, and the positive and negative feedbacks on ecosystem variables.

Ward and Stanford (1995b) modelled connectivity in progressively larger river reaches (Fig. 1.1). While the Macquarie and Tooms Rivers both fit into their mountain headwater reach category, lateral connectivity in the Macquarie River is much stronger than their model predicted. Riparian litter abundance was highest in both rivers in summer (Fig. 7.2, left panel), but was out of phase with benthic litter abundance at the Macquarie River sites (Fig. 7.2, right panel). A spate generated overbank flows in the Macquarie River after heavy rain in August 2007, but benthic litter abundance was higher at all sites. Lateral transport relies on overland runoff in Tooms River, where spates are rare, but separating

the apparent effects of flow regulation from the impacts of the drought is challenging. Drought conditions can reduce infiltration of rainfall into hydrophobic clay soils (Doerr *et al.* 2000), which are typical of these sites, increasing overland flow and potentially increasing litter transport.

There has been limited research into the lateral transfer of leaf litter between the riparian zones and the benthos in low order confined rivers, with the focus on the litter dynamics of floodplain rivers (e.g. Francis and Sheldon 2002). Future research should initially establish whether the low lateral connectivity shown for Tooms River is a result of flow regulation or an effect of the drought. If this effect remains in the absence of drought, the extent of the reduction could be quantified, with regular monitoring of litter traps in the riparian zone, and simultaneous sampling of benthic litter traps, with nets across and above the stream to monitor downstream transport and vertical litter fall. This would establish the strength of lateral, longitudinal and vertical connectivity between the riparian zone and the benthos, and potentially suggest modifications to the flow regime to increase connectivity, and hence nutrient cycling.

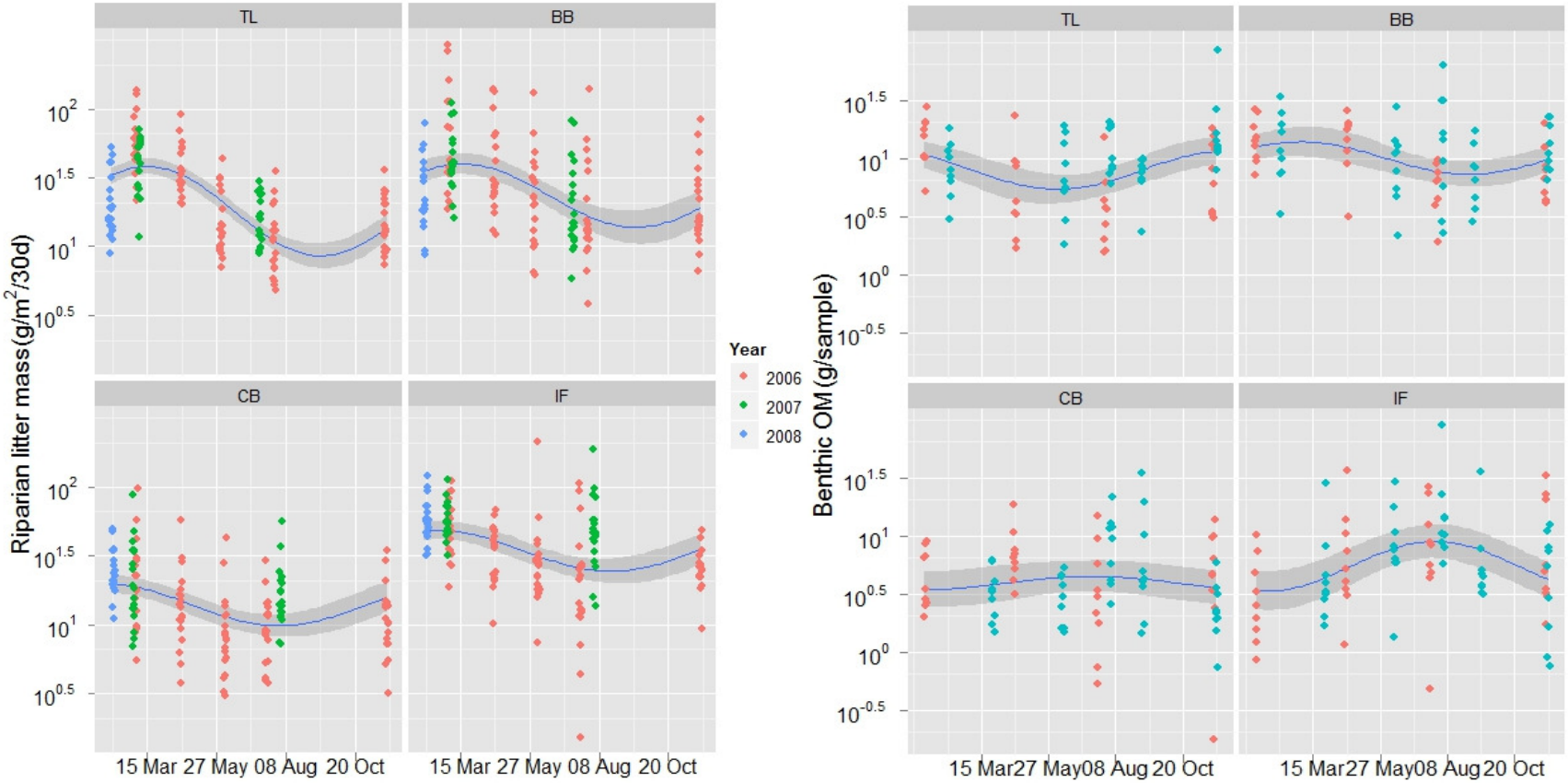


Figure 7.2 Log_{10} riparian leaf mass accumulation (g.m^2 per 30 days) (left panel) and log_{10} benthic organic material (g. sample) (right panel) for all study sites, commencing January 2006. TL and BB are the upstream and downstream sites on Tooms River; CB and IF are the upstream and downstream sites on the Macquarie River, respectively. Dots represent individual sediment mats or samples, with the year of collection indicated by the colours in the legend. The blue line shows the periodic regression trend over the full study period, with 95% confidence intervals in grey.

Many comparative studies of the biofilm communities below dams are confounded by cold water releases and hydro-power peaking, which may also explain some of the discrepancies between the macroinvertebrate communities in Tooms River and other studies. Biofilms were more abundant in Tooms River, as predicted, but the unexpectedly high levels of autotrophy warrant further investigation. Higher taxonomic resolution of the biofilm communities, targeting bacterial and fungal components, may help explain the lack of seasonal variation in biofilm abundance.

The macroinvertebrate communities of the two rivers were expected to converge with the drought, towards a common dominance by tolerant taxa. Surprisingly, invertebrates from the adjacent Macquarie River did not colonise the downstream Tooms River site, BB, when the flow was low enough to support lentic habitats. Even strong dispersers, such as Odonata, did not colonise this site, although they were generally present in the Macquarie River. Future research should concentrate on establishing the biological factors influencing the dispersal and recruitment of key taxa, in contrast to the observational studies generally reported (e.g. Cortes *et al.* 2002). For example, population genetic techniques could determine if particular genotypes (e.g. from small founder populations), are restricted to the Macquarie River, with low genetic diversity limiting their environmental tolerances.

It is also possible that the dispersal ability of many taxa has been overestimated, and that significant barriers to colonisation exist. Factors such as poor water quality in Tooms River may limit establishment of some taxa. It would be necessary to establish which aspects of the water quality (such as turbidity or nutrient concentrations) are important to individual taxa, or indeed if there are other barriers to recruitment. The dispersal, arrival and colonisation of key invertebrate taxa could be assessed using traps close to the stream

channels and at various distances into the riparian zone, along with simultaneous sampling of benthic habitats and physicochemical variables, to establish recruitment patterns and cohort structure.

7.2 Assessing the impact of flow regulation on invertebrate diversity

At the family level of identification, benthic invertebrate diversity is lower in Tooms River, so greater differences would be expected at the species level. However, family level taxonomy is used in most river assessment studies and is the basis for river health monitoring schemes such as AUSRIVAS and RIVPACS, which compare the taxa observed at a site with taxa expected to be present. However, Usseglio-Polatera *et al.* (2000) showed that detection of anthropogenic impacts could be limited by poor knowledge of invertebrate life history traits and environmental tolerances.

This suggests that a trait-based approach to invertebrate distribution patterns may be more appropriate. This method is based on the habitat template principles of Southwood (1977, 1988), which proposed that the physical conditions of a site would determine the life history and physical characteristics of the taxa present in that habitat. Townsend *et al.* (1997a) amended this approach to show that species traits were a good indicator of the disturbance regime of a site, and thus a useful adjunct to regular functional feeding group and community composition assessments, while Growns and Davis (1994) allocated species to flow requirement groups to assess the effect of modified flows on invertebrate community abundances. Miller *et al.* (2010) found that species traits were a better indication of irrigation withdrawal impacts than diversity indices, but acknowledged that many traits were correlated with each other, as were some physical variables which were not always ecologically significant.

The ELOHA framework (Poff *et al.* 2010) proposed using species-level life histories to assess regulation impacts. However, while this approach is useful for fish or plants, it is difficult to employ with hundreds of invertebrate species, each with different tolerances and preferences. Such approaches rely on characterisation of species life histories, diets, tolerances and morphological attributes (e.g. Usseglio-Polatera *et al.* 2000; Poff *et al.* 2006). As Statzner and Bêche (2010) point out, large species trait databases are mainly restricted to Europe and North America, whereas a trait-based approach to invertebrate distributions is more difficult in Australia, where the life histories of many taxa are unknown (Marchant 1986; Growns and Growns 2001). Although Statzner and Bêche (2010) cited several studies where there were inconsistencies between invertebrate abundances and trait-based assessments, they recommended using a limited number of traits related to pre-determined stressors, with standardised definitions and descriptions of species traits. Such an approach would give a better indication of the factors influencing the taxa present in Tooms River, and clarify the full extent of flow regulation effects.

7.3 Management of anti-drought in regulated rivers

Water infrastructure requires a large investment, which should be matched by more targeted research into the downstream effects of flow regulation (Downes 2010), so that cost benefit analyses are based on appropriate scientific evidence. Based on the results of this study, it seems reasonable to speculate that a long-term anti-drought flow regime will have substantial effects on in-stream biodiversity for many kilometres downstream of the impoundment. This may have widespread, deleterious effects on riverine biodiversity. For example the Tasmanian Irrigation Development Board website (http://www.tidb.com.au/) currently lists 13 proposals for dams, of similar characteristics to the Tooms storage, in the drier areas of Tasmania.

The management of diversity in regulated rivers has focussed on fostering recovery downstream of a dam (e.g. Nichols *et al.* 2006; Bond *et al.* 2008). Although Petts (1987) proposed that there would be ecosystem recovery when the catchment downstream of the dam was more than 40% of the total catchment, recovery may be difficult to assess. For Tooms River, this requires a catchment in excess of 155 km^2 below Tooms Lake. As several studies have found (e.g. Miller *et al.* 2010), both land use and river 'style' (Brierley and Fryirs 2000) change with distance from the headwaters, so that downstream recovery, in a taxonomic sense, may never be achievable. This implies that it may not be possible to mitigate the effects of anti-drought flow regulation.

7.4 Management to optimise ecosystem services

Maintaining ecosystem services (i.e. the health and diversity of ecological components) in regulated rivers can be a challenge for river managers. Although this study and some others (e.g. Chester and Norris 2006; Reich *et al.* 2009) have shown that there can be some downstream recovery from the impacts of a dam, any chance at recovery to pre-impoundment condition would require determination of an appropriate flow regime, based on real-time unregulated conditions and accurate monitoring of the effectiveness of changes. As SKM (2010) point out, there is a lack of accuracy in modelled low flows, because it is difficult to calculate runoff when catchment soils are dry, or where hydrophobic soils develop (e.g. Doerr *et al.* 2000). Improved models are needed to reduce the current difficulty to detect low flows and cease-to-flow events in the Macquarie system, because there are no operational flow gauges in the catchment above Tooms River. Moreover, flow records are compromised by unmetered abstractions between Tooms River and the gauge at Trefusis. Reinstatement of the flow gauge at the existing v-notch weir at Longmarsh in the upper catchment would allow meaningful assessment of water availability (SKM 2010), so that

decisions on irrigation releases are based on natural, rather than modified flows.

In the interim, partial restoration of a variable flow regime could improve invertebrate diversity and reduce biofilm abundance in Tooms River, as was shown in the Broken – Boosey Creek system in Victoria, where pipelines delivered water to downstream irrigators, avoiding anti-droughts and restoring natural cease-to-flow events (Reich *et al.* 2009). Pulses of high flows and cease-to-flow periods were incorporated in environmental flows in the Loddon River in Victoria in 2006 (Bond *et al.* 2008), while variable flow releases increased invertebrate diversity and reduced biofilm abundance in the Cotter River (Chester and Norris 2006). Although overbank flows can only occur in Tooms River when the full dam spills, occasional flushing flows could reduce biofilm abundance and turbidity, with clearer water and clean substrates, potentially removing some of the current barriers to higher invertebrate diversity, and generally improving ecosystem health. Figure 7.3 shows the potential ecosystem benefits of allowing some summer low flows and restoring winter and spring flushing flows.

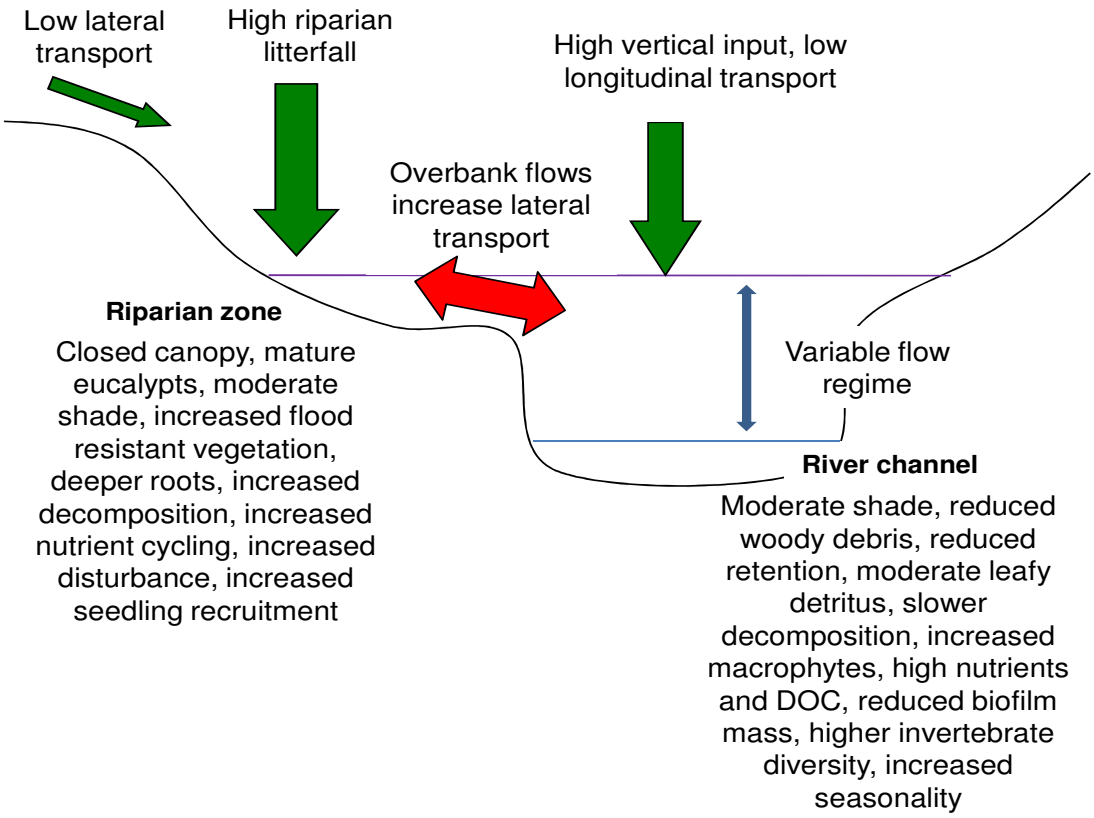


Fig. 7.3 Conceptual model of the modified dynamics of riparian and benthic resources, and their influence on ecosystem services and invertebrate communities, in response to a variable flow regime in Tooms River.

The Macquarie River above the junction with Tooms River is the only surviving section of the natural river system. Reinstatement of a more variable flow regime to Tooms River would provide ecological benefits to Tooms River and to the downstream Macquarie River. However, regular monitoring of invertebrate communities, and biofilm abundances and taxonomic composition, would be essential to evaluate the effectiveness of these changes to the flow regime, and to allow for further modifications to the regime to maximise ecosystem recovery.

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Appendix 1: Standing stock of riparian leaf litter SIMPER analyses by site

SIMPER average abundance scores between sites for the standing stock of riparian leaf litter, showing the square root transformed average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that species to the similarity, and cumulative percentage to the total abundance, for each study site

	Average abundance	Average similarity	Std. Dev.	Contribution %	Cumulative %
Tooms River - Site TL		Average similarity between samples: 73.59			
Other	2.83	21.66	3.00	29.44	29.44
Eucalyptus spp.	2.65	19.13	2.76	26.00	55.43
Acacia spp.	2.26	16.95	3.10	23.03	78.46
Leptospermum spp.	1.30	9.86	3.93	13.40	91.86
Tooms River - Site BB		Average similarity between samples: 73.70			
Eucalyptus spp.	2.84	20.79	4.28	28.20	28.20
Acacia spp.	2.76	19.49	3.65	26.45	54.65
Other	2.48	17.53	3.24	23.79	78.44
Sedges	1.48	6.17	0.87	8.37	86.80
Leptospermum spp.	0.96	5.84	1.48	7.92	94.73
Macquarie River – Site CB		Average similarity between samples: 76.08			
Acacia spp.	3.13	23.52	3.88	30.91	30.91
Other	2.96	21.89	4.29	28.77	59.68
Eucalyptus spp.	1.57	9.49	2.07	12.48	72.16
Leptospermum spp.	1.09	7.16	2.10	9.41	81.57
Notelaea ligustrina	0.70	3.89	0.94	5.11	86.68
Grasses	0.65	3.47	0.83	4.56	91.24
Macquarie River - Site IF		Average similarity between samples: 69.66			
Acacia spp.	3.10	19.79	3.32	28.40	28.40
Other	2.00	12.13	3.51	17.42	45.82
Eucalyptus spp.	1.90	10.87	2.06	15.60	61.42
Leptospermum spp.	1.24	7.67	5.40	11.01	72.43
Allocasuarina sp.	1.24	5.18	1.02	7.43	79.86
Juncus sp.	1.19	4.48	0.89	6.43	86.30
Sedges	1.05	3.90	0.93	5.60	91.89

Appendix 1. SIMPER average abundance scores between the regulated and unregulated rivers for the standing stock of riparian leaf litter, showing the square root transformed average abundance within samples, average similarity between sites, standard deviation from the mean, the percentage contribution of that species to the similarity, and cumulative percentage to the total abundance, for each river (continued)

	Average abundance	Average similarity	Std. Dev.	Contribution %	Cumulative %
Regulated sites TL & BB		Average similarity between sites: 71.67			
Eucalyptus spp.	2.75	20.02	3.28	27.93	27.93
Other	2.65	19.39	3.04	27.06	54.99
Acacia spp.	2.52	18.11	3.23	25.27	80.26
Leptospermum spp.	1.13	7.63	1.99	10.65	90.90
Unregulated sites CB & IF		Average similarity between sites: 69.03			
Acacia spp.	3.11	21.75	3.47	31.51	31.51
Other	2.50	16.30	2.93	23.62	55.12
Eucalyptus spp.	1.73	10.08	1.99	14.61	69.73
Leptospermum spp.	1.16	7.43	2.77	10.76	80.49
Sedges	0.89	3.42	0.83	4.96	85.45
Notelaea ligustrina	0.68	3.31	0.86	4.80	90.25

Appendix 2: Riparian leaf mass SIMPER analysis by site and collection round

SIMPER average abundance scores between sites for the riparian litter abundance, standardised to 30 day time periods, showing the square root transformed average abundance of each leaf type within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that leaf type to the similarity, and cumulative percentage to the total abundance, for each collection round. The category 'Other' includes unidentified organic material and leaf fragments.

Leaf type	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Round 1 – summer 2005 - 06					
	Tooms River Site TL: Average similarity: 74.48				
Leptospermum spp.	3.37	21.23	3.83	28.50	28.50
Eucalyptus spp.	2.58	14.88	2.02	19.97	48.47
Other	2.21	13.36	2.98	17.94	66.42
Acacia mucronata	1.84	10.53	2.43	14.14	80.56
Leptospermum flowers	1.26	7.24	2.25	9.73	90.28
	Tooms River Site BB: Average similarity: 68.98				
Eucalyptus spp.	3.47	19.69	2.25	28.55	28.55
Other	2.00	11.64	3.15	16.88	45.43
Leptospermum spp.	2.16	11.60	2.05	16.82	62.26
Acacia mucronata	2.21	11.52	1.76	16.70	78.96
Leptospermum flowers	1.00	4.60	1.18	6.67	85.63
Other spp.	0.84	4.38	1.25	6.35	91.98
	Macquarie River Site CB: Average similarity: 71.29				
Leptospermum spp.	2.95	18.71	3.66	26.25	26.25
Eucalyptus spp.	2.74	15.25	2.43	21.39	47.64
Acacia mucronata	2.58	14.80	2.13	20.77	68.41
Other	1.63	9.93	2.98	13.93	82.34
Leptospermum flowers	1.16	7.04	2.47	9.87	92.21
	Macquarie River Site IF: Average similarity: 70.16				
Leptospermum spp.	3.26	18.99	2.43	27.07	27.07
Acacia mucronata	2.26	12.80	3.04	18.24	45.31
Other	1.79	10.82	3.06	15.42	60.74
Leptospermum flowers	1.05	7.10	10.50	10.12	70.86
Eucalyptus spp.	1.53	5.57	0.84	7.94	78.79
Allocasuarina sp.	1.00	4.09	0.97	5.83	84.62
Juncus sp.	1.16	3.98	0.74	5.68	90.30

Appendix 2. SIMPER average abundance scores between sites for the riparian litter abundance, standardised to 30 day time periods, showing the square root transformed average abundance of each leaf type within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that leaf type to the similarity, and cumulative percentage to the total abundance, for each collection round. The category 'Other' includes unidentified organic material and leaf fragments (continued).

Leaf type	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Round 2 – late summer 2005-06					
	Tooms River Site TL: Average similarity: 69.67				
Leptospermum spp.	3.26	22.17	2.80	31.82	31.82
Eucalyptus spp.	2.79	17.82	2.45	25.58	57.40
Other	2.00	13.9	2.79	19.96	77.36
Acacia mucronata	1.42	9.16	2.03	13.15	90.51
	Tooms River Site BB: Average similarity: 50.79				
Leptospermum spp.	2.32	13.27	1.30	26.12	26.12
Other	1.79	11.03	1.27	21.71	47.83
Eucalyptus spp.	1.89	8.88	0.83	17.49	65.31
Acacia mucronata	1.53	8.08	1.05	15.91	81.22
Sedges	1.53	5.63	0.60	11.08	92.30
	Macquarie River Site CB: Average similarity: 64.69				
Leptospermum spp.	2.47	17.03	1.83	26.32	26.32
Acacia mucronata	2.42	16.53	1.79	25.56	51.88
Other	2.21	16.26	2.40	25.13	77.01
Eucalyptus spp.	2.11	11.87	1.24	18.34	95.35
	Macquarie River Site IF: Average similarity: 65.12				
Leptospermum spp.	3.63	25.57	2.56	39.27	39.27
Acacia mucronata	1.95	10.95	1.73	16.82	56.09
Juncus sp.	1.58	7.44	0.96	11.42	67.51
Other	1.16	7.33	2.60	11.26	78.77
Eucalyptus spp.	1.00	3.78	0.72	5.80	84.56
Grasses	0.74	3.43	0.76	5.27	89.84
Round 3 – autumn 2006					
	Tooms River Site TL: Average similarity: 67.03				
Leptospermum spp.	3.11	22.16	1.98	33.06	33.06
Other	2.74	21.98	4.72	32.79	65.86
Acacia mucronata	1.74	11.98	1.97	17.87	83.73
Eucalyptus spp.	1.68	5.42	0.56	8.08	91.81
	Tooms River Site BB: Average similarity: 55.50				
Other	2.26	14.92	2.27	26.88	26.88
Leptospermum spp.	2.21	12.87	1.51	23.18	50.07
Eucalyptus spp.	2.16	9.84	0.82	17.73	67.80
Acacia mucronata	1.74	9.48	1.20	17.09	84.88
Other spp.	0.58	2.97	0.68	5.35	90.23
	Macquarie River Site CB: Average similarity: 63.29				
Other	2.68	23.87	4.62	37.72	37.72
Acacia mucronata	2.63	19.87	1.76	31.4	69.12
Leptospermum spp.	2.11	14.41	1.58	22.77	91.89

Appendix 2. SIMPER average abundance scores between sites for the riparian litter abundance, standardised to 30 day time periods, showing the square root transformed average abundance of each leaf type within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that leaf type to the similarity, and cumulative percentage to the total abundance, for each collection round. The category 'Other' includes unidentified organic material and leaf fragments

Leaf type	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
	Macquarie River Site IF: Average similarity: 64.32				
Leptospermum spp.	2.68	16.48	2.23	25.63	25.63
Acacia mucronata	2.37	14.21	2.67	22.10	47.73
Other	1.89	12.51	2.84	19.45	67.18
Juncus sp.	1.37	5.21	0.82	8.10	75.28
Grasses	0.89	4.56	1.22	7.10	82.38
Allocasuarina sp.	1.00	3.91	0.83	6.07	88.45
Eucalyptus spp.	1.16	3.10	0.49	4.83	93.28
Round 4 – late winter 2006					
	Tooms River Site TL: Average similarity: 64.97				
Leptospermum spp.	3.00	22.45	1.50	34.56	34.56
Other	2.47	21.54	3.68	33.16	67.72
Acacia mucronata	1.37	8.20	1.09	12.62	80.33
Other spp.	0.89	7.11	1.51	10.95	91.28
	Tooms River Site BB: Average similarity: 57.11				
Other	2.63	19.6	3.27	34.32	34.32
Eucalyptus spp.	2.53	13.64	1.08	23.89	58.21
Leptospermum spp.	1.95	10.83	1.18	18.96	77.17
Acacia mucronata	1.53	8.02	1.07	14.04	91.21
	Macquarie River Site CB: Average similarity: 64.60				
Other	3.42	29.40	3.93	45.5	45.50
Acacia mucronata	2.58	17.67	1.75	27.35	72.85
Leptospermum spp.	1.53	10.32	2.02	15.98	88.83
Eucalyptus spp.	1.16	3.44	0.46	5.33	94.16
	Macquarie River Site IF: Average similarity: 62.70				
Leptospermum spp.	2.63	16.65	2.69	26.56	26.56
Other	2.37	14.86	3.14	23.69	50.25
Acacia mucronata	1.84	9.07	1.33	14.47	64.72
Grasses	1.26	6.19	1.23	9.88	74.60
Sedges	1.53	5.74	0.74	9.16	83.75
Eucalyptus spp.	1.42	5.34	0.83	8.51	92.26
Round 5 – early summer 2006-07					
	Tooms River Site TL: Average similarity: 72.89				
Other	2.58	17.36	3.59	23.81	23.81
Leptospermum flowers	2.32	15.32	3.22	21.02	44.83
Leptospermum spp.	2.37	13.82	1.51	18.96	63.80
Eucalyptus spp.	2.32	13.24	1.84	18.16	81.95
Acacia mucronata	1.32	7.96	2.13	10.92	92.87

Appendix 2. SIMPER average abundance scores between sites for the riparian litter abundance, standardised to 30 day time periods, showing the square root transformed average abundance of each leaf type within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that leaf type to the similarity, and cumulative percentage to the total abundance, for each collection round. The category 'Other' includes unidentified organic material and leaf fragments

Leaf type	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Tooms River Site BB: Average similarity: 58.29					
Leptospermum spp.	2.32	14.34	1.49	24.60	24.60
Other	1.68	10.69	2.09	18.35	42.95
Leptospermum flowers	1.84	10.30	1.15	17.68	60.63
Acacia mucronata	1.53	7.73	1.07	13.27	73.90
Eucalyptus spp.	1.68	7.43	1.02	12.75	86.65
Other spp.	0.74	4.57	1.05	7.84	94.49
Macquarie River Site CB: Average similarity: 66.93					
Other	2.68	21.55	5.76	32.20	32.20
Acacia mucronata	2.58	17.80	1.88	26.59	58.79
Leptospermum spp.	1.84	11.12	1.61	16.62	75.41
Eucalyptus spp.	1.47	9.96	2.03	14.88	90.30
Macquarie River Site IF: Average similarity: 70.59					
Leptospermum spp.	2.74	17.53	2.90	24.84	24.84
Leptospermum flowers	2.37	14.43	2.51	20.45	45.28
Other	1.89	11.41	2.69	16.16	61.45
Acacia mucronata	1.84	10.03	2.43	14.20	75.65
Other spp.	1.00	5.28	1.47	7.48	83.13
Juncus sp.	1.16	4.04	0.81	5.72	88.85
Round 6 – late summer 2006-07					
Tooms River Site TL: Average similarity: 73.45					
Leptospermum spp.	3.21	21.99	2.63	29.94	29.94
Eucalyptus spp.	2.53	17.49	3.05	23.81	53.75
Other	2.53	17.01	2.66	23.15	76.91
Acacia mucronata	1.58	9.48	1.53	12.91	89.81
Tooms River Site BB: Average similarity: 62,21					
Other	2.42	15.65	3.06	25.16	25.16
Leptospermum spp.	2.63	13.44	1.27	21.60	46.76
Acacia mucronata	2.32	12.57	1.52	20.21	66.97
Eucalyptus spp.	1.89	9.83	1.56	15.80	82.77
Other spp.	0.79	3.68	0.90	5.92	88.69
Sedges	0.95	2.88	0.63	4.63	93.32
Macquarie River Site CB: Average similarity: 65.00					
Leptospermum spp.	2.68	16.32	2.00	25.11	25.11
Other	2.26	15.77	2.87	24.27	49.37
Acacia mucronata	2.53	15.75	1.74	24.23	73.60
Eucalyptus spp.	1.74	10.16	1.83	15.63	89.24

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Leaf type	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Macquarie River Site IF Average similarity: 70.15					
Leptospermum spp.	3.63	24.43	3.01	34.82	34.82
Acacia mucronata	2.79	18.39	2.81	26.22	61.04
Other	1.47	9.75	2.92	13.90	74.94
Eucalyptus spp.	1.32	5.64	0.96	8.04	82.97
Other spp.	0.84	4.88	1.24	6.96	89.94
Round 7 – winter 2007					
Tooms River Site TL: Average similarity: 70.39					
Leptospermum spp.	3.11	23.45	3.76	33.32	33.32
Eucalyptus spp.	2.58	15.05	1.23	21.38	54.69
Other	2.05	14.38	2.59	20.42	75.12
Acacia mucronata	1.63	10.95	2.65	15.56	90.68
Tooms River Site BB: Average similarity: 64.41					
Other	2.21	15.59	4.76	24.21	24.21
Leptospermum spp.	2.53	14.33	1.60	22.25	46.46
Acacia mucronata	2.26	13.16	2.17	20.44	66.89
Eucalyptus spp.	2.11	10.93	1.32	16.96	83.86
Other spp.	0.74	3.59	0.90	5.58	89.43
Macquarie River Site CB: Average similarity: 71.65					
Other	2.79	20.62	3.23	28.77	28.77
Acacia mucronata	2.79	19.51	2.69	27.23	56.00
Leptospermum spp.	1.89	12.02	2.29	16.78	72.78
Other spp.	1.11	8.78	9.84	12.26	85.04
Eucalyptus spp.	1.47	8.41	1.58	11.73	96.77
Macquarie River Site IF: Average similarity: 65.76					
Leptospermum spp.	3.42	21.98	2.57	32.54	32.54
Other	2.00	11.98	2.37	17.74	50.28
Acacia mucronata	1.95	10.99	2.13	16.27	66.54
Eucalyptus spp.	1.47	7.64	1.32	11.31	77.86
Other spp.	1.26	7.14	1.67	10.57	88.43
Grasses	0.95	5.66	1.48	8.38	96.81
Round 8 – summer 2007-08					
Tooms River Site TL: Average similarity: 73.99					
Eucalyptus spp.	3.00	21.46	2.60	29.25	29.25
Leptospermum spp.	2.95	20.78	3.04	28.32	57.56
Other	1.79	12.97	3.00	17.67	75.23
Acacia mucronata	1.47	10.01	3.58	13.64	88.87
Other spp.	0.74	3.87	0.91	5.27	94.14

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Leaf type	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Tooms River Site BB: Average similarity: 64.37					
Eucalyptus spp.	2.84	18.19	3.22	28.26	28.26
Other	2.00	11.61	2.34	18.04	46.30
Leptospermum spp.	2.16	10.62	1.66	16.50	62.80
Acacia mucronata	1.63	7.94	1.27	12.34	75.13
Sedges	1.63	7.07	1.21	10.99	86.12
Leptospermum flowers	0.79	4.06	1.05	6.31	92.43
Macquarie River Site CB: Average similarity: 72.31					
Other	2.42	18.90	6.02	26.14	26.14
Acacia mucronata	2.21	15.61	2.40	21.59	47.73
Leptospermum spp.	1.89	12.33	2.68	17.05	64.78
Eucalyptus spp.	1.47	7.89	0.98	10.91	75.69
Leptospermum flowers	1.05	7.83	2.80	10.82	86.52
Grasses	0.79	5.36	1.25	7.41	93.92
Macquarie River Site IF: Average similarity: 72.76					
Other	2.63	17.67	4.54	24.29	24.29
Acacia mucronata	2.53	15.29	3.03	21.01	45.30
Leptospermum spp.	2.47	14.71	2.27	20.21	65.51
Eucalyptus spp.	1.58	8.74	1.98	12.01	77.53
Other spp.	1.16	7.12	2.48	9.79	87.32
Juncus sp.	0.95	3.83	0.86	5.26	92.58

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Appendix 4: Invertebrate total abundances, functional feeding groups and flow preferences by site

Invertebrate taxa, functional feeding group (FFG), flow preference group (FPG) and total abundance (*N*) per study site. In the FFG column, CG = collector-gatherer, F = filterer, P = predator, Sc/G = scraper-grazer, Sh = shredder. In the FPG column, A = flow avoider, F = flow facultative, O = flow obligate

Order or Class	Family	FFG	FPG	Unregulated sites *N*		Regulated sites *N*	
				CB	IF	TL	BB
Decapoda	Atyidae	CG	A	23	16	0	0
	Parastacidae	CG	F	2	0	0	0
Amphipoda	Ceinidae	CG	F	1201	271	459	8
Isopoda	Janiridae	Sh	F	23	3	0	0
	Uramphisopinae	Sh	F	83	8	0	15
Copepoda		CG	A	228	347	5676	22
Ostracoda		F	A	154	1830	436	252
Cladocera	Chydoridae	CG	A	0	676	240	5
Plecoptera	Eusthenidae	P	F	156	1	0	362
	Gripopterygidae	CG	F	3707	359	4855	1582
	Notenomouridae	CG	F	386	211	0	371
Ephemeroptera	Baetidae	Sc/G	F	81	57	3	966
	Caenidae	CG	A	91	42	17	1
	Leptophlebiidae	CG	F	2796	1849	10	3001
Megaloptera	Sialidae	P	F	0	0	0	49
Coleoptera	Curculionidae	CG	F	0	0	0	1
	Dytiscidae	P	F	79	10	1	10
	Elmidae	CG	O	161	257	19	303
	Haliplidae	CG	A	1	0	0	0
	Hydrochidae	CG	A	0	0	0	1
	Hydrophilidae	P	F	1	0	1	0
	Psephenidae	Sc/G	F	263	27	3	682
	Scirtidae	Sc/G	F	79	99	0	11
	Staphilinidae	CG	F	0	0	1	2
Hemiptera	Corixidae	P	A	35	1	1	1
	Gerridae	P	A	36	1	0	0
	Mesovellidae	P	A	2	5	0	0
	Vellidae	P	A	1	5	0	1
	Hemiptera spp.	P	A	0	0	0	2

Appendix 4: Invertebrate taxa, functional feeding group (FFG), flow preference group (FPG) and total abundance (*N*) per study site (continued)

Order or Class	Family	FFG	FPG	Unregulated sites *N*		Regulated sites *N*	
				CB	IF	TL	BB
Diptera	Athericidae	P	O	2	0	0	96
	Ceratopogonidae	P	A	33	65	13	181
	Chaoboridae	P	A	0	0	1	0
	Culicidae	F	A	1	33	0	0
	Dolichopododinae	P	F	3	5	0	0
	Empididae	P	O	78	80	7	316
	Ephydridae	CG	A	1	4	3	0
	Non-Tanypodinae	CG	A	2823	5133	5499	5954
	Sciomyzidae	P	A	0	3	0	6
	Simuliidae	F	O	158	3077	2130	268
	Tabanidae	P	A	0	0	0	2
	Tanyderidae	Sh	F	10	26	70	169
	Tanypodinae	P	A	944	1212	401	770
	Thaumaleidae	Sc/G	F	0	0	0	3
	Tipulidae	Sh	A	3	13	1	39
Lepidoptera	Crambidae	Sh	F	1	1	4	2
Trichoptera	Atriplectides	P	A	0	1	0	14
	Calamoceratidae	CG	F	12	10	0	0
	Calocidae	Sh	F	39	11	1	258
	Conoesucidae	CG	O	1	0	0	21
	Ecnomidae	P	F	59	27	3	185
	Glossosomatidae	CG	F	2	0	0	1
	Helicopsychidae	CG	F	3	0	0	4
	Hydrobiosidae	P	O	49	204	116	268
	Hydropsychidae	F	O	0	5	2	64
	Hydroptilidae	CG	F	450	134	215	121
	Leptoceridae	Sh	A	62	260	4	240
	Odontoceridae	Sh	F	0	1	2	5
	Philorheithridae	P	O	2	5	0	114
	Polycentropodidae	P	A	11	46	0	14
	Tasimiidae	Sc/G	O	1	0	0	0
	Trichoptera spp.	CG	F	21	33	20	153
Neuroptera	Sisyridae	P	A	0	4	0	0
Odonata	Gomphidae	P	F	0	0	0	1
	Lestidae	P	A	1	2	1	0
	Macromidae	P	F	0	0	1	0
	Protoneuridae	P	A	0	1	0	0
	Synthemistidae	P	F	1	13	0	0
	Telephlebiidae	P	F	3	13	10	29
	Zygoptera sp	P	A	1	12	0	0

Appendix 4: Invertebrate taxa, functional feeding group (FFG), flow preference group (FPG) and total abundance (*N*) per study site (continued)

Order or Class	Family	FFG	FPG	Unregulated sites *N*		Regulated sites *N*	
				CB	IF	TL	BB
Oligochaeta	Oligochaeta	CG	A	236	502	432	649
Nematoda	Nematoda	P	A	37	203	1464	74
Nematomorpha	Giordiidae	P	F	1	23	5	15
Turbellaria		CG	O	23	23	430	18
Hirudinea	Hirudinea	P	F	21	32	14	0
Gastropoda	Ancylidae	Sc/G	A	27	32	776	10
	Glacidorbidae	Sc/G	O	20	46	1940	0
	Hydrobiiidae	Sc/G	O	4621	2722	3723	2078
	Physidae	Sc/G	F	2	70	2640	82
	Planorbidae	Sc/G	O	82	16	198	2
Bivalvia	Sphaeridae	F	F	53	42	2	33
Arachnida	Hydracarina	P	F	500	466	3689	805
Total				19990	20704	35558	20722

Appendix 5: Invertebrate functional feeding groups (FFG) by site and season, SIMPER analyses

SIMPER average abundance scores between sites for the invertebrate functional feeding groups, showing the square root transformed average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that group to the similarity, and cumulative percentage to the total abundance, for each collection round

Functional Feeding group	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Round 1 - January 2006					
Tooms River Site TL: Average similarity: 81.70					
Scrapers	23.35	44.49	6.43	54.46	54.46
Predators	9.74	15.65	5.10	19.16	73.61
Collectors	9.73	14.48	6.11	17.73	91.34
Tooms River Site BB: Average similarity: 84.36					
Collectors	17.75	33.03	4.87	39.15	39.15
Predators	9.79	19.64	10.44	23.28	62.43
Scrapers	10.84	19.40	3.10	23.00	85.43
Filterers	3.78	6.55	3.94	7.76	93.19
Macquarie River Site CB: Average similarity: 74.71					
Collectors	23.89	33.93	5.51	45.42	45.52
Scrapers	13.67	18.08	3.98	24.20	69.62
Predators	10.96	14.97	6.02	20.03	89.65
Shredders	3.20	4.99	2.98	6.68	96.33
Macquarie River Site IF: Average similarity: 71.30					
Collectors	12.98	27.42	6.41	38.45	38.45
Predators	9.09	19.20	5.23	26.92	65.38
Filterers	7.63	10.38	2.03	14.56	79.93
Scrapers	7.75	7.32	1.16	10.26	90.20
Round 2 - April 2006					
Tooms River Site TL: Average similarity: 78.83					
Collectors	30.57	39.96	5.04	50.69	50.69
Scrapers	18.03	19.08	4.12	24.21	74.89
Predators	10.07	9.82	2.65	12.46	87.35
Filterers	8.77	9.59	4.47	12.16	99.51
Tooms River Site BB: Average similarity: 87.74					
Collectors	18.24	34.33	12.13	39.13	39.13
Scrapers	13.30	22.68	5.48	25.85	64.98
Predators	9.06	17.49	12.30	19.93	84.91
Shredders	4.97	8.84	8.55	10.08	94.99
Macquarie River Site CB: Average similarity: 76.71					
Scrapers	15.84	40.16	7.92	52.35	52.35
Collectors	9.51	22.71	3.81	29.60	81.96
Predators	3.60	7.82	3.99	10.20	92.16
Macquarie River Site IF: Average similarity: 74.35					
Collectors	9.83	30.72	10.17	41.32	41.32
Predators	5.93	19.17	7.80	25.79	67.11
Filterers	5.17	10.52	1.96	14.16	81.26
Scrapers	4.40	9.98	3.96	13.42	94.68

Appendix 5: SIMPER average abundance scores between sites for the invertebrate functional feeding groups, showing the square root transformed average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that group to the similarity, and cumulative percentage to the total abundance, for each collection round (continued)

Functional Feeding group	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Round 3 - July 2006					
	Tooms River Site TL: Average similarity: 78.87				
Collectors	13.36	31.91	6.32	40.47	40.47
Scrapers	12.12	27.48	6.70	34.84	75.30
Predators	6.97	15.08	4.79	19.12	94.42
	Tooms River Site BB: Average similarity: 81.27				
Collectors	22.29	39.67	8.66	48.81	48.81
Predators	9.32	17.15	5.71	21.10	69.92
Scrapers	6.07	11.12	9.07	13.69	83.61
Shredders	5.41	8.51	3.47	10.47	94.08
	Macquarie River Site CB: Average similarity: 72.25				
Collectors	9.16	33.32	7.48	46.12	46.12
Scrapers	9.99	26.78	2.52	37.07	83.18
Predators	2.57	9.67	2.42	13.38	96.56
	Macquarie River Site IF: Average similarity: 69.48				
Collectors	8.18	24.95	3.71	35.91	35.91
Scrapers	11.22	23.38	1.22	33.65	69.56
Filterers	3.22	9.45	3.75	13.60	83.16
Predators	3.61	9.18	5.03	13.21	96.37
Round 4 - November 2006					
	Tooms River Site TL: Average similarity: 80.59				
Scrapers	19.42	33.50	8.24	41.57	41.57
Collectors	16.31	25.43	12.23	31.56	73.13
Predators	11.23	15.33	6.82	19.02	92.15
	Tooms River Site BB: Average similarity: 86.91				
Collectors	9.34	33.35	28.79	38.37	38.37
Predators	6.60	22.44	10.44	25.82	64.19
Scrapers	5.05	16.42	6.52	18.89	83.08
Shredders	2.61	8.24	22.16	9.48	92.56
	Macquarie River Site CB: Average similarity: 74.38				
Collectors	23.28	34.21	4.50	45.99	45.99
Scrapers	14.21	17.41	2.29	23.40	69.39
Predators	9.52	13.62	4.49	18.32	87.70
Filterers	5.01	6.17	1.90	8.29	95.99
	Macquarie River Site IF: Average similarity: 75.14				
Collectors	24.22	34.13	9.27	45.42	45.42
Scrapers	15.64	15.28	1.89	20.33	65.75
Predators	12.26	15.20	7.38	20.23	85.98
Filterers	8.84	9.07	2.14	12.07	98.06

Appendix 5: SIMPER average abundance scores between sites for the invertebrate functional feeding groups, showing the square root transformed average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that group to the similarity, and cumulative percentage to the total abundance, for each collection round (continued)

Functional Feeding group	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Round 5 - March 2007					
		Tooms River Site TL: Average similarity: 84.34			
Collectors	11.94	27.27	8.70	32.34	32.34
Scrapers	11.88	26.47	6.05	31.38	63.72
Predators	9.16	18.81	3.36	22.30	86.02
Filterers	4.11	9.61	4.73	11.40	97.42
		Tooms River Site BB: Average similarity: 79.21			
Collectors	24.55	35.58	4.58	44.92	44.92
Predators	10.21	15.39	6.19	19.43	64.34
Scrapers	8.11	12.86	8.27	16.24	80.58
Shredders	5.26	8.75	3.29	11.04	91.62
		Macquarie River Site CB: Average similarity: 77.30			
Collectors	17.10	42.83	9.14	55.41	55.41
Predators	5.88	13.22	3.72	17.10	72.51
Scrapers	6.73	12.69	2.02	16.42	88.93
Filterers	3.17	4.93	1.52	6.37	95.30
		Macquarie River Site IF: Average similarity: 80.52			
Collectors	16.67	45.87	5.77	56.97	56.97
Predators	5.58	15.44	4.41	19.17	76.14
Filterers	4.36	9.65	2.47	11.99	88.13
Scrapers	3.89	6.27	2.94	7.79	95.92
Round 6 - June 2007					
		Tooms River Site TL: Average similarity: 81.28			
Collectors	24.40	35.06	9.78	43.14	43.14
Predators	16.40	24.39	8.77	30.01	73.15
Filterers	9.75	10.59	2.51	13.03	86.18
Scrapers	7.94	8.75	4.87	10.76	96.94
		Tooms River Site BB: Average similarity: 85.09			
Collectors	14.01	38.47	12.84	45.21	45.21
Predators	8.04	20.20	7.90	23.74	68.96
Scrapers	4.36	11.32	9.53	13.31	82.27
Shredders	3.70	10.05	11.42	11.82	94.08
		Macquarie River Site CB: Average similarity: 78.25			
Collectors	17.40	43.85	5.90	56.03	56.03
Scrapers	6.86	15.78	4.37	20.17	76.20
Predators	4.83	10.14	3.57	12.96	89.17
Filterers	3.93	7.20	2.37	9.20	98.37
		Macquarie River Site IF: Average similarity: 81.21			
Filterers	21.98	40.24	5.39	49.55	49.55
Collectors	12.87	22.05	4.69	27.16	76.71
Predators	6.60	11.53	4.17	14.19	90.90

Appendix 5: SIMPER average abundance scores between sites for the invertebrate functional feeding groups, showing the square root transformed average abundance within samples, average similarity between samples, standard deviation from the mean, the percentage contribution of that group to the similarity, and cumulative percentage to the total abundance, for each collection round (continued)

Functional Feeding group	Average abundance	Average similarity	Standard deviation	Contribution %	Cumulative %
Round 7 - September 2007					
		Tooms River Site TL: Average similarity: 83.78			
Collectors	17.02	36.77	6.46	43.88	43.88
Scrapers	10.09	22.11	21.18	26.39	70.28
Predators	10.93	19.99	5.63	23.86	94.14
		Tooms River Site BB: Average similarity: 81.64			
Collectors	12.50	38.39	10.82	47.02	47.02
Predators	7.04	23.04	9.65	28.22	75.24
Scrapers	4.87	12.97	3.22	15.89	91.13
		Macquarie River Site CB: Average similarity: 75.44			
Collectors	14.78	40.48	6.33	53.66	53.66
Scrapers	6.51	19.96	4.93	26.45	80.11
Predators	4.74	10.57	2.94	14.02	94.13
		Macquarie River Site IF: Average similarity: 85.38			
Collectors	16.66	39.53	10.09	46.30	46.30
Predators	9.18	22.75	11.81	26.65	72.95
Filterers	6.92	13.92	4.61	16.31	89.26
Scrapers	3.38	7.03	5.59	8.24	97.50
Round 8 - November 2007					
		Tooms River Site TL: Average similarity: 82.63			
Collectors	29.50	38.10	13.30	46.11	46.11
Predators	13.05	15.91	3.68	19.25	65.36
Filterers	14.43	15.80	6.21	19.13	84.49
Scrapers	8.92	11.18	3.83	13.53	98.02
		Tooms River Site BB: Average similarity: 88.46			
Collectors	16.97	34.63	11.08	39.15	39.15
Predators	10.92	22.02	13.44	24.89	64.05
Scrapers	8.05	14.46	5.06	16.34	80.39
Filterers	6.10	12.42	10.00	14.04	94.43
		Macquarie River Site CB: Average similarity: 70.82			
Collectors	17.70	42.68	5.92	60.26	60.26
Predators	7.59	13.78	1.59	19.45	79.71
Filterers	3.20	6.86	2.37	9.69	89.40
Shredders	1.97	5.55	4.13	7.84	97.24
		Macquarie River Site IF: Average similarity: 82.70			
Collectors	16.41	31.50	9.38	38.09	38.09
Filterers	12.82	22.48	6.52	27.19	65.28
Predators	9.13	18.23	7.91	22.04	87.32
Scrapers	6.01	8.80	2.40	10.64	97.96